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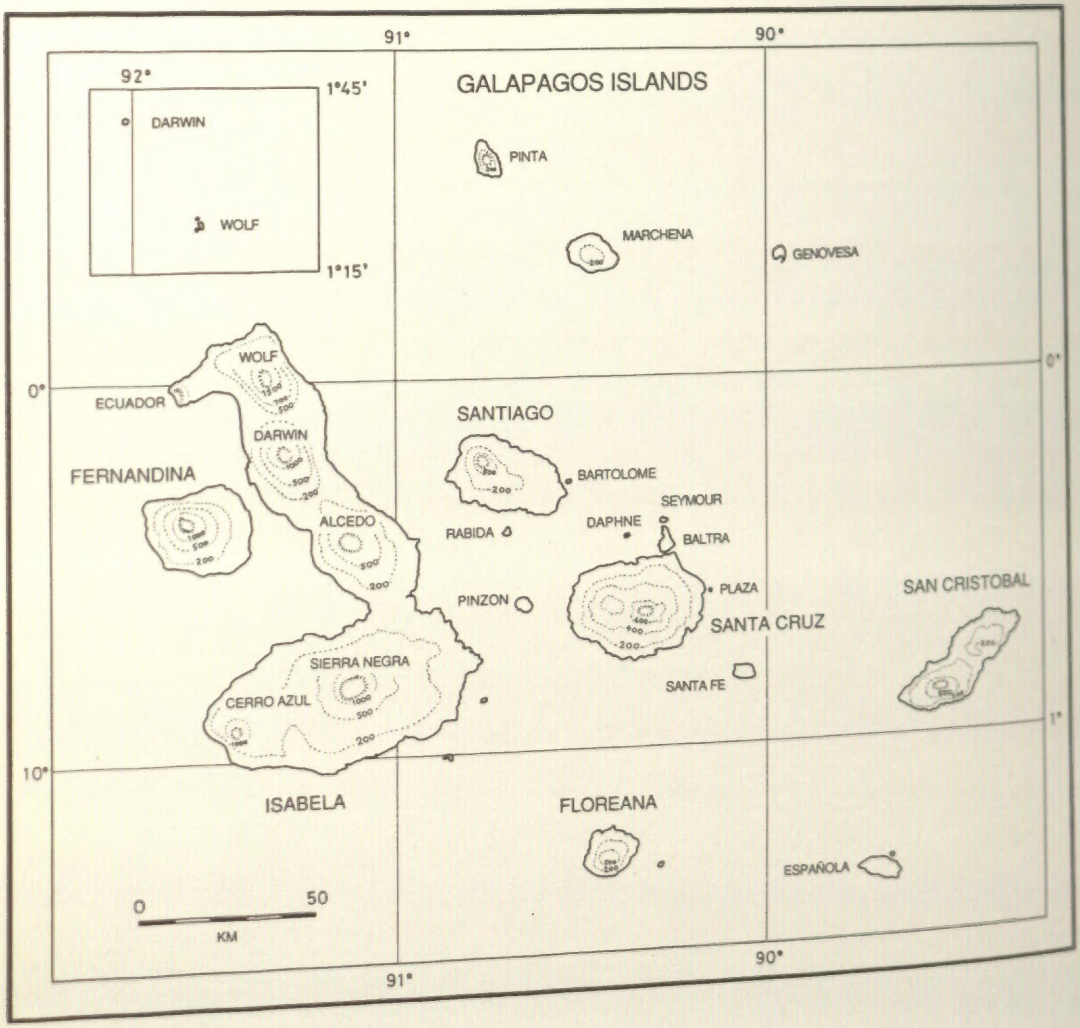
BOTANICAL RESEARCH AND MANAGEMENT IN GALAPAGOS

Proceedings of the Workshop on Botanical Research and Management in Galápagos held 11–18 April 1987 at the Charles Darwin Research Station, Santa Cruz, Galápagos, Ecuador

Edited by
J.E. Lawesson, O. Hamann, G. Rogers, G. Reck, and H. Ochoa

Missouri Botanical Garden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CONTENTS

Introduction for the Proceedings of the Botanical Research and Management in Galápagos Workshop, 11–18 April 1987
Günther K. Reck & Humberto Ochoa ix

The Workshop on Botanical Research and Management in the Galápagos Islands, 11–18 April 1987
Ole Hamann & Jonas E. Lawesson xi

INTRODUCTION TO GALAPAGOS

Taxonomic Status and Needs
Duncan M. Porter 1

Research and Management in the Galápagos: Some Botanical Considerations
Ole Hamann 5

Threatened Plants in Galápagos
Henning Adsersen 11

Alien Plants in the Galápagos Islands, a Summary
Jonas E. Lawesson 15

BOTANICAL RESEARCH

Some Unique Ecological Aspects of Oceanic Island Ecosystems
Dieter Mueller-Dombois & Lloyd L. Loope 21

Species of Amaranthaceae in the Galápagos Islands and Their Affinites to Species on the South American Mainland
Uno H. Eliasson 29

Reproductive Biology of Galápagos Islands Angiosperms
Conley K. McMullen 35

Herbaceous and Ericaceous Communities in the Highlands of Santa Cruz, the Galápagos Islands
Syuzo Itow 47

Undisturbed Vegetation on Fernandina, 1964
F. R. Fosberg 59

Intra-archipelago Distribution Patterns of Vascular Plants in Galápagos
Henning Adsersen 67

Ferns as Indicators of Vegetation Types in the Galápagos Archipelago
Henk van der Werff 79

Satellite Images: a Tool in Vegetation Studies, Conservation, and Management in Galápagos
Marlene Meyer & Henning Adsersen 93

Mapping and Classifying Vegetation in the Galápagos Islands, Some Considerations
I. A. E. Atkinson 101

Cartografía de la Vegetación en las Islas Galápagos
Charles Huttel 117

A Two-year Study of Post-fire Vegetation Dynamics on Southern Isabela, Galápagos Islands, Ecuador
J. Bosco Nowak, Jonas E. Lawesson, Henning Adsersen & Tjitte de Vries 123

The Dynamics of *Scalesia cordata* (Asteraceae) in Different Habitats in Sierra Negra, Isabela, Galápagos
Tjitte de Vries & Arnaldo Tupiza 137

Permanent Vegetation Quadrats in Galápagos
Henning Adsersen 149

Threatened Plant Species and Priority Plant Conservation Sites in the Galápagos Islands
Jonas E. Lawesson 153

The Impact of Introduced Herbivores on the Galápagos Rail (*Laterallus spilonotus*)
Daniel K. Rosenberg 169

Plant-Animal Interactions: Consumption of Seeds by Darwin's Finches
P. R. Grant & B. R. Grant 179

INTRODUCED ORGANISMS

Strategies for Limiting the Invasion of Protected Areas by Introduced Organisms
I. A. W. Macdonald 189

Plantas Introducidas en las Islas Galápagos
Jonas E. Lawesson & Luis Ortiz 201

Managing the Invasions of Alien Ungulates and Plants in Hawaii's Natural Areas
C. P. Stone & R. A. Holt 211

Weed Management in Hawaii's National Parks
Clifford W. Smith 223

The Role of Herbicides in Managing Conservation Lands
Philip S. Motooka 235

MANAGEMENT OF SUSTAINABLE RESOURCES

Conservación y Manejo de la Vegetación en Galápagos
Miguel Cifuentes Arias 243

The Colonization of San Cristóbal, Galápagos Islands—a Historical Perspective
Jacinto Gordillo 247

Management and Research Efforts to Protect Vulnerable Endemic Plant Species of Haleakala National Park, Maui, Hawaii
Lloyd L. Loope & Arthur C. Medeiros 251

Revegetation on Bikini Atoll, 1985
F. R. Fosberg 265

Approaches to Plant Conservation

The World Conservation Monitoring Centre and Threatened Island Floras
Stephen D. Davis 271

Plant Conservation Priorities Worldwide—the IUCN-WWF Approach
Ole Hamann 279

Combined Recommendations from the Workshop: Botanical Research and Management in Galápagos
Jonas E. Lawesson, Ole Hamann & Juan Black 291

Participant List 297

INTRODUCTION FOR THE PROCEEDINGS OF THE BOTANICAL RESEARCH AND MANAGEMENT IN GALAPAGOS WORKSHOP, 11–18 APRIL 1987

There is certainly no need to convince the readers of these proceedings of the scientific significance of the Galápagos Islands and the importance of conserving their resources and protecting what is unique about their wildlife. However, the general public is probably much less aware that Galápagos plants are as distinct from the neighboring continental flora as the islands' animals are from the continental fauna.

All driving forces and elements of organic evolution, characterized by such processes as adaptive radiation and interisland speciation can be observed among plants and are more transparent to scientists here than in large land areas. Biogeographical conditions and constraints make islands the best study cases for evolutionary processes. Among archipelagos, the Galápagos are recognized to have one of the largest proportions of still undisturbed natural conditions.

The easily recognizable differences between the islands and between their species and communities give them their unique scientific and educational value. The islands' climatological conditions allow for extraordinarily diversified biological zones. Each of these zones has its own unique species and communities.

Human settlers, of course, will colonize the zones that present suitable environmental conditions for agriculture. They will selectively alter and cultivate areas where soil and precipitation guarantee adequate food production. These areas are more likely to lose their original plant communities to a much larger degree than other areas. Exactly this has happened on some of the islands, such that only relatively small remnants of the large *Scalesia* forests, or the "brown zone" vegetation, have been preserved.

The Ecuadorian government has done much to preserve the archipelago in the long term by protecting 97% of the islands' surface as a national park. However, the human population of the islands has more than doubled during the last several years, from less than 4,000 inhabitants to at least 8,000. The demand on natural resources available within the islands is growing. Newcomers cast their gaze toward the areas within the national park that still seem to offer arable soils. They may not understand that the plant communities surviving there are not repeated on uninhabited islands, simply because those islands do not present the same conditions.

Human settlements are a reality, and settlers rightfully demand possibilities for suitable development. How can this be achieved without endangering important and unique features of the islands?

Due to poor land use within the areas assigned to agriculture, the islands do not feed their inhabitants. However, are the islands fertile enough to make further rural development desirable?

At present, most vegetable food must be brought from the mainland by ship or by plane. Seeds are introduced also, but many of them are infested with fungi and other diseases.

Many plants introduced by humans in the past have grown into pests. Where settlers do not alter communities by direct action, guayaba, quinine trees, *Lantana*, and *Eugenia* are rapidly replacing the natural vegetation. Introduced herbivores are destroying whole areas down to the roots—and accelerating irreversible erosion—even in areas where life for humans is impossible due to lack of water.

Are there ways of effectively fighting these threats? Is eradication of alien species possible, or must long-term control and management strategies be developed? If it is possible to combat these

threats, where should we start, what are the minimum areas, and which native communities are the most endangered?

Whereas the Galápagos National Park Service has been extremely successful in eradicating some of the vertebrate pests on the smaller islands and in containing them on some of the larger ones, so far there is no efficient control over the continuous introduction of new invertebrates, insects, plant and animal diseases, and aggressive new plant species. In the long run, it is the human population that will suffer most from the consequences.

Managers have a great responsibility to make decisions with long-term effects and to act on what is feasible, even if the means are limited. It is crucial to make the right decision and not to concentrate on activities that do not lead to positive results.

It seemed necessary to gather specialists—those who had described the unique features of Galápagos plants and vegetation and who know what is critical—to interchange information and to make concrete recommendations for management. Certain questions must be answered in order to improve management: what further research must be done, what additional information do we urgently need? It is necessary to bring together experts in pest control and to discuss ways of making progress against the spread of introduced species and diseases, or at least to avoid losing the battle. The knowledge gathered so far must be reviewed and recommendations made for long-term monitoring.

The Galápagos National Park Service and the Charles Darwin Research Station have placed great hopes on this workshop, the first of its kind ever organized in the Galápagos Islands. The recommendations of the workshop participants will not only be used by those two institutions, however, but also by those involved in development and land use planning. No immediate results will be achieved. The recommendations of this workshop will gradually be reflected in all future plans for research and management in the Galápagos Islands.

GÜNTHER K. RECK, CDRS
HUMBERTO OCHOA, SPNG

THE WORKSHOP ON BOTANICAL RESEARCH AND MANAGEMENT IN THE GALAPAGOS ISLANDS, 11–18 APRIL 1987[1]

Ole Hamann[2] and Jonas E. Lawesson[3]

This volume presents the first attempt to compile botanical information of particular relevance for managing and conserving the flora of the Galápagos Islands. It comprises the majority of papers presented at the International Workshop on Botanical Research and Management in the Galápagos, organized by the Charles Darwin Research Station (CDRS) and the Galápagos National Park Service (SPNG), 11–18 April 1987. Unless otherwise stated in the papers, the plant names follow Wiggins & Porter's *Flora of the Galápagos Islands* (1971).

Eighty-eight scientists, managers, and naturalists from ten different countries gathered in the Galápagos to discuss and explore how the disciplines of the botanical sciences can be translated into practical conservation management. The recommendations for future actions formulated by the workshop participants are included at the end of this volume.

In 1985 the Charles Darwin Foundation (CDF) and the recently appointed Director of the CDRS, Dr. Günther Reck, agreed that it was high time to develop a comprehensive plan for conserving the flora and vegetation of the Galápagos Islands. It was recognized that, while much has been achieved with respect to conserving unique animal species and ecosystems since the creation of the National Park and the CDF in 1959, the conservation of plants and vegetation had been somewhat neglected. Being a marine biologist rather than a botanist, Dr. Günther Reck stressed the need for getting together the botanists and managers with experience in the Galápagos and in relevant areas elsewhere so that they could review the existing research data on Galápagos botany and help prepare guidelines for the CDRS and the SPNG to follow in meeting the growing threats to the unique plant life on the islands. Consequently, the International Workshop on Botanical Research and Management in the Galápagos was organized.

[1]We are deeply indebted to many institutions and individuals who made the workshop and the publishing of the proceedings possible. Our most sincere thanks go to the John D. and Catherine T. MacArthur Foundation, Chicago, for the very generous grant, which covered the considerable costs involved. We are extremely grateful for all the encouragement and outstanding support received from Dr. Peter H. Raven and Dr. George Rogers of the Scientific Publications Department at the Missouri Botanical Garden, from the planning of the workshop to editing and publishing the papers presented. For logistic help we thank TAME Airlines, the Instituto Nacional de Galápagos (INGALA), and the municipality of Santa Cruz. We are grateful for the excellent simultaneous translation provided by Turisa Williams, Congresos Ecuador, and for workshop items kindly donated by Metropolitan Tours. The Smithsonian Institution and the International Union for Conservation of Nature and Natural Resources (IUCN) are thanked for much help and advice during preparation of the workshop. Many people helped make the workshop successful. Ms. Myriam Burneo, Orion Travels, Quito, and Mr. Ramón Andrade, CDRS, arranged the travel to and from Galápagos most efficiently. The staffs of the CDRS and the SPNG worked tremendously hard in preparing and running the workshop: Ms. Sylvia Harcourt, Mr. Carlos Vacacela, Mr. Juan Black, Ms. Marta Parra, Ms. Gayle Davis, Mr. Eduardo Arboleda, and Mr. Felipe Cruz particularly helped in coordinating the event. We are extremely grateful to all of them and to all other helpers too numerous to mention. The Botanical Institute, University of Aarhus, is gratefully acknowledged for support and provision of working facilities during the preliminary editing of this volume.

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FIGURE 1. In 1971 the Galápagos National Park Service succeeded in eliminating feral goats on the island of Santa Fe. By then the vegetation was very open with *Opuntia echios* var. *barringtonensis* as the most conspicuous species, as shown in this photo from 1972. Since the goats were removed, a notable regeneration of the vegetation has been recorded.

The plight of the Galápagos flora has become increasingly obvious during the last decade. It is true, as Dr. Peter Kramer, former President of the CDF, stated, that "no other archipelago is at once so extensive, so isolated, so simple in its ecosystems and so little altered by man"; yet, the biological isolation of the islands and their ecosystems ended with the human colonization, and for more than a century humans have been modifying the ecosystems of Galápagos. Following the human colonization, many areas of closed, native forests were opened or transformed into pastures, crop fields, and plantations or were otherwise altered. Domestic animals and plants were brought to the islands, and many ran wild with the result that the major threat to the indigenous ecosystems today are feral mammals and introduced, exotic plants. The islands now have a record of species introductions followed by habitat alterations and destructions comparable to that documented in such other parts of the world as Hawaii and New Zealand.

The most obvious and immediate conservation problems are caused by feral goats, pigs, donkeys, cats, and dogs: feral goats and pigs have already pushed some of indigenous plant species close to extinction and have destroyed native vegetation types. The impact of these animals on the native flora and vegetation is often rapid and devastating, and conservation actions are called for immediately.

Even more serious impacts may result from the growing number of aggressive, alien plant species, which are spreading in the archipelago. Invasion of areas formerly occupied by native

plants by several introduced plant species is facilitated by the disturbances caused by feral mammals. Even worse, a small but growing number of alien plant species are gradually or rapidly displacing native plant species from natural vegetation. In the long term this may turn out to be the gravest conservation problem in the Galápagos and the most difficult to solve. The number of introduced plants now amounts to roughly 240 species, of which perhaps 50 are actively invading natural areas. Feral mammals and aggressive alien plants are threatening perhaps as many as 100 native plant taxa, particularly on the larger, inhabited islands, and they threaten several indigenous and unique vegetation types. The aggressive plants also present a serious problem in the farming areas outside the National Park by preventing a rational land use, e.g., for livestock.

Overexploitation of the limited timber resources of the islands is another problem: the need for timber has resulted in selective logging of certain native tree species in the dry parts of the larger islands, thereby reducing their populations considerably. The vegetation, of which these species form an integral part, is threatened and its natural reproduction and regeneration has been found to decrease.

The higher, mesic areas, comprising some of the most diverse environments in the Galápagos, are partly taken over by agriculture. The remaining portion of the higher mesic areas are located outside the Colonized Zone and are thus included in the National Park. They merit special attention, not the least because such areas are the first to be infested with aggressive, alien species.

These problems have been recognized for quite some time by the CDRS and the SPNG. At various occasions in the past, recommendations have been made in order to intensify the conservation work on plants and vegetation, as for example in 1980, when the CDF made an assessment of the previous 20 years' work and outlined the priorities for the next 10 years. However, the available funds, manpower, and expertise have never been adequate to tackle these problems on an archipelago scale.

This then is the context within which the April 1987 workshop assumes its importance, and a set of ambitious objectives was formulated:

1. To compile the existing data on the Galápagos flora and vegetation and its dynamics. The studies undertaken by means of transects and permanent quadrats will be of special interest.
2. To assess the present status of the Galápagos flora and vegetation, followed by a classification by priority of certain areas, vegetation types, or taxa in need of urgent preservation measures.
3. To assess the changes and threats to the Galápagos vegetation presented by human activities, including the impact of introduced organisms.
4. To develop an appropriate management program for the next 10–15 years, particularly focusing on the threats to the flora and vegetation, such as introduced organisms.
5. To discuss the feasibility of utilizing exotic plant species in the Galápagos, and, if possible, to develop a plan for such utilization.
6. To discuss and outline areas of research in botany, forestry, and conservation biology that need to be strengthened during the coming 10–15 years.
7. To discuss the status of the Galápagos Islands as a biosphere reserve and as a World Heritage Site.
8. To discuss how the experiences and lessons from Galápagos conservation and management can be applied in other island groups.

During the first two days of the workshop, 44 papers were presented; they form the basis of this volume. On the third day an excursion to the island of Floreana to place for observation on the grave problems caused by *Psidium guajava* and *Lantana camara* on this island. The following two days were devoted to working in five groups on specific topics, while the last day included a general session for discussion of the results from the working groups and for drafting the general recommendations, which are annexed in this volume.

The papers in this book are grouped into five sections, each of importance for meeting the objectives outlined above. The first section sets the scene by introducing some basic subjects of

FIGURE 2. Highland of Santa Cruz. A few individuals of *Scalesia pedunculata* (left) and open pampa vegetation without trees. Areas like this are most susceptible to invasion by aggressive alien plants, such as *Cinchona succirubra*.

relevance for the conservation of the Galápagos flora and vegetation. The second section comprises research papers focusing on recent investigations, particularly in the Galápagos. The subjects treated range from taxonomy and ecology to vegetation mapping, conservation biology, biogeography, and other areas. These first sections indicate the present status of our knowledge of the plants of Galápagos, and they emphasize subjects of direct relevance for management in the islands. Introduced organisms are of such importance that one section is devoted to this subject, and the experiences from other parts of the world are brought to bear on the Galápagos situation. The fourth section then treats specific management practices and measures for conserving plants and vegetation

in the Galápagos and in other island groups. The fifth section is composed of papers treating approaches to conservation in more general terms and on a larger scale.

For obvious reasons it was not the intention to publish the detailed results of the deliberations of each of the working groups mentioned above, but rather to present the general recommendations, on which the participants agreed. However, the detailed reports from each working group were presented to the CDRS and the SPNG, and together with the recommendations, these reports formed the basis for a subsequent development of a plant conservation program for the Galápagos Islands. This program is a plan of action for the next 15 years and consists of a basic part, which covers the urgent and immediate needs, and an extended part, which includes, for example, elements of agro-forestry and schemes for utilization of native and exotic timber resources.

Thus, it is a great pleasure to note that thanks to the knowledge, enthusiasm, and hard work of the participants, the general objective of the workshop was met, so that the CDRS and the SPNG now have a short- and medium-term program for plant conservation in the Galápagos Islands. The next step forward will be to secure the funds necessary and implement this program.

TAXONOMIC STATUS AND NEEDS

Duncan M. Porter[1]

ABSTRACT

Recommendations for research on Galápagos Islands plants published in 1972 and progress on them are discussed. The most progress has been made in phytogeography, with lesser amounts in ecological studies. Increased knowledge of island taxa and their distributions mandates publication of a new Flora.

In October 1972, the conference "Galápagos Science: Status and Needs" was held at the Smithsonian Institution in Washington, D.C. Working groups at the conference prepared reports on marine science, plants, terrestrial vertebrates, terrestrial invertebrates, birds, paleontology, conservation, and collections. Since the *Flora of the Galápagos Islands* (Wiggins & Porter, 1971) was then recently published, much of the report on plants (by Charles Rick, William Reeder, Ira Wiggins, and Duncan Porter) discussed ecology, not systematics. Areas of proposed research were (1) vegetation mapping and quantitative sampling ("top priority"), (2) plant–animal interrelationships ("this and following recommendations are second order priority"), (3) phytogeography, (4) reproductive ecology, and (5) population structure.

At the end of the general discussion and prior to the meetings of the working groups, I made the following points regarding the vascular plants: "I'd like to mention three fields—three types of studies that have not as yet been mentioned and that impinge both on botany and ecology and are thus interdisciplinary in nature: (1) a detailed study of pollination and pollinators, (2) a study of plant dispersal mechanisms, and (3) a study of phytogeographical relationships, both within the archipelago and between it and mainland South America. Now that the *Flora* has been completed, much of the basic information is available to pursue such studies. They should be given priority on any list of botanical projects for the Galapagos" (Simkin et al., 1973, p. 32). I took my own advice regarding plant dispersal mechanisms (Porter, 1983) and phytogeographical relationships with other areas (Porter, 1976, 1984a), but further work on interisland relationships has not been published.

Studies of life history phenomena, including pollination and pollinators, on the other hand, have been taxon-based, rather than being general floristic surveys. Genera examined include *Acalypha* (Hamann, 1979b), *Bursera* (Clark & Clark, 1981), *Croton* (Downhower & Racine, 1976; Hamann, 1979b), *Lycopersicon* (Rick & Forbes, 1975; Rick, 1983), *Macraea* (Eliasson, 1984), *Miconia* (Hamann, 1979c), *Opuntia* (Racine & Downhower, 1974; Grant & Grant, 1981), and *Scalesia* (Hamann, 1979a). Most recently, however, a study of insect visitors to flowers has begun to bear fruit (McMullen, 1985, 1986a), as has one of seed germination (McMullen, 1986b). These should lead to a comprehensive survey of flowering, pollinators, pollination mechanisms, and seed production. Such a survey still is badly needed for the Galápagos. This remains a primary goal of systematic research in the islands.

The *Flora* included 702 species, subspecies, and varieties of vascular plants, both native and introduced. By 1984 at least 736 taxa (541 indigenous, 195 introduced) were known, and more have been added since. Adsersen (1989) gives the number of indigenous species as 570. There are questions as to whether some taxa thought to be introduced might actually be native (cf. Porter, 1983, and Adsersen, 1989). In addition, a number of genera with endemic species have been

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FIGURE 1. *Scalesia pedunculata*, one of the most famous and characteristic trees in Galápagos, now severely threatened on Santiago and San Cristóbal islands. (Photo taken by J. E. Lawesson.)

revised since the *Flora* was published, resulting in the recircumscription of some taxa and the recognition of others as new. These genera include *Acalypha* (Seberg, 1984), *Chamaesyce* (Huft & van der Werff, 1985), *Darwiniothamnus* (Lawesson & Adsersen, 1986), *Lecocarpus* (Adsersen, 1980), *Scalesia* (Eliasson, 1974; Hamann & Wium-Andersen, 1986), *Tiquilia* (=*Coldenia*, Richardson, 1977), and those of the Amaranthaceae (Eliasson, 1985). In addition, *Darwiniothamnus*, *Lecocarpus*, and *Scalesia* (Fig. 1) are endemic. A number of other taxa have been revised as well, leading to many name changes in Galápagos plants.

At the 1972 conference, Ira Wiggins urged that biosystematic studies be directed toward "the genera *Scalesia*, *Alternanthera*, and members of the Cyperaceae, Euphorbiaceae, Convolvulaceae and Gramineae (Poaceae)—plus several others—many valuable results can confidently be expected." (Simkin et al., 1973, p. 14). In the 15 years since this statement was made, some have been studied, others not. Further research should be pursued on all genera with endemic taxa, particularly those 19 where adaptive radiation has taken place (Porter, 1979). Further investigation of the flora of mainland Ecuador continues to diminish the number of endemics previously recognized (Porter, 1984b), but this is more or less balanced by the description of new endemic taxa (e.g., Hamann & Wium-Andersen, 1986; Lawesson & Adsersen, 1986). Wiggins also urged that cytotaxonomical, anatomical, and morphological investigations be emphasized, areas that still remain little explored.

The *Flora* is now 16 years old and badly in need of revision because of the tremendous amount of research on Galápagos plants that its publication stimulated. The Stanford University Press has been approached regarding a second edition and has responded favorably. However, it is my

intention to produce a second edition that is more like John Thomas's *Flora of the Santa Cruz Mountains of California* (Thomas, 1961) than the 1971 edition of the *Flora*. That is, I think that a manual of the flora of the islands that can be easily taken into the field is now called for, rather than another large research publication that is most useful on the herbarium desk. Such a manual would contain keys, limited synonymy, short morphological descriptions of taxa, ecology, geographical distributions, and illustrations of selected taxa. The introduction would cover climate, history, plant ecology, and other aspects of the islands. This is another primary goal of systematic research in the archipelago.

In this paper I have emphasized studies on the vascular plants of the Galápagos, as they are my own areas of expertise. However, I wish to make clear that such research is just as important for other groups, such as the algae, bryophytes, lichens, and fungi. Perhaps it is even more important, since they are more poorly known in the islands than are the vascular plants.

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RESEARCH AND MANAGEMENT IN THE GALAPAGOS: SOME BOTANICAL CONSIDERATIONS

Ole Hamann[1]

ABSTRACT

On the background of the conceptual framework presented by the World Conservation Strategy, the basic importance of plants and vegetation to all other life on earth is emphasized, and the need to apply botanical knowledge to solve conservation problems is stressed. The shared characteristics of biota on oceanic islands, and the fragility and vulnerability of island ecosystems are briefly discussed. Previous botanical research in the Galápagos is well documented and recent literature reviews are mentioned. The change of emphasis in the setting of priorities for botanical research in the Galápagos Islands, from basic to more applied and conservation-orientated studies, as presented by the Charles Darwin Foundation for the Galápagos Isles (CDF) and the Galápagos National Park Service (SPNG) during the last two decades, is discussed; the most obvious research areas of relevance for the long-term conservation of the Galápagos flora and vegetation are outlined.

> Plants are a primary resource of fundamental importance for human life. Rapid population growth, together with the excessive and increasing demands that are placed on the world's resources by our societies, are threatening to destroy a major portion of our common heritage of plants. This threat is especially evident in the tropics and subtropics, where at least two-thirds of the plants of the world occur, and where the process of deforestation is proceeding at an alarming rate. Widespread poverty, famine, and political instability, for example in Africa, are manifestations of the same processes that are driving plants to extinction and, by doing so, seriously limiting our future options for developing sustainable relationships between man and his living resources.
>
> All human beings depend upon plants, directly or indirectly, for their lives, as do most other forms of life: at least four million different kinds of organisms depend on about 250.000 kinds of plants. But unless we immediately begin to take drastic and innovative measures to preserve them, it is likely that tens of thousands of plant species will disappear forever during our lives or those of our children. Their loss would amount to a fundamental and permanent change in the character of life on earth, a life whose wealth is characterized by great diversity. (Conclusions of the IUCN-WWF Plant Advisory Group meeting, St. Louis, Missouri, 17–18 December 1984.)

It is hardly an exaggeration that one of the most important tasks facing mankind as the 21st century approaches is to ensure the conservation in perpetuity of what is left of the natural ecosystems of the world. Yet conservation organizations have tended to neglect plants even though they are essential to human and animal life, and provide the fabric of vegetation and landscape. At the same time, botanists have to a large degree been slow to appreciate the urgency of the crisis facing the plant world and of the need to place their knowledge and expertise at the service of conservation.

On this background, IUCN and WWF launched an International Plants Conservation Programme in 1984, to focus global attention on the plight of the plants and plant communities of the world (IUCN, WWF, 1984; see also Hamann, this volume). The Programme builds on the basis of the World Conservation Strategy (IUCN/UNEP/WWF, 1980), which links conservation with development so that human use of the biosphere can be managed in such a way as to "yield the greatest sustainable benefit to present generations while maintaining its potential to meet the needs and aspirations of future generations." The major objectives of conservation reflected in the World Conservation Strategy are: to maintain essential ecological processes and life-support systems, to

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preserve genetic diversity, and to ensure that any utilization of species and ecosystems is sustainable. In ecological terms, this may roughly mean to maintain ecosystem functioning and structure and to ensure sound ecosystem management. The question of how botanical research can contribute to achieve these objectives is of the greatest importance for plant conservation in general and of particular importance to the present workshop on the Galápagos Islands.

The "Insular Syndrome"

Carlquist (1974) identified an "insular syndrome" characteristic for island biotas or waif biotas. Based on factors of dispersal and evolution, he outlined and analyzed 24 principles, including such concepts as disharmonic composition of floras and faunas; rapid adaptive evolution as the inevitable result when a small number of immigrants meet a broad spread of ecological opportunities; evolution of new growth forms among plants, gigantism, dwarfism, and other variations, in island animal forms; and decreased competitive ability among endemics.

In terms of importance to conservation, a range of the characteristics of oceanic islands and of their biota is of particular interest:

The high degree of endemism, which results in islands making a disproportionately large contribution to the diversity of species and ecosystems of the world.

The peculiar adaptions, e.g., loss of dispersal ability for plants or flightlessness among birds, poorly prepare the organisms for survival in the face of habitat changes, human interference, or exotic herbivores or predators, increasing their vulnerability to extinction.

Islands are seldom well endowed with natural resources, which are scarce in variety and quantity, and thus are particularly liable to overexploitation and mismanagement. Islands are environmentally fragile.

Because of the scarcity, fragility, and vulnerability of natural resources, islands require different approaches to ensure a continuous flow of raw materials, goods, and services needed by their inhabitants.

In many oceanic islands, people have tended to develop their own ways and means to conserve natural resources, but new pressures from population growth, tourism, and political factors often surpass the capacities of traditional methods to maintain a balance between people and resources.

Islands face important and unique difficulties but provide at the same time a resource for improving approaches to conservation management. Indeed, pilot projects or new demonstration schemes carried out in islands under relatively simple conditions where the limits to the ecosystems are clear may point to solutions to problems also faced on larger, continental scales. Therefore, islands like the Galápagos share not only problems but also opportunities with other oceanic islands.

Research in the Galapagos

Ever since Charles Darwin visited the archipelago in 1835 during his famous voyage around the world on H.M.S. Beagle, the Galápagos Islands have been recognized for their unique scientific value. Since then, they have attracted naturalists from all over the world. The flora and vegetation have been the object of many investigations.

A landmark was reached in 1971 with the publication of the *Flora of the Galápagos Islands* by

Wiggins & Porter. The *Flora* sums up the very detailed knowledge on the taxonomy of Galápagos plants then available, building on all previous investigations and synthesized through the work of the 1964 Galápagos International Scientific Project and through the work of the many specialists coauthoring the *Flora*. In addition, it gives an excellent account of the history of botanical exploration, deals in some detail with vegetation zones, and treats geology, climate, and other subjects. In short, the *Flora* by Wiggins & Porter created the basis for expanding the botanical research into plant ecology, in the broadest sense.

The 1972 Galápagos Science Conference (Simkin et al., 1972) brought together researchers and managers to analyze the status of Galápagos science and to identify the more important needs for interdisciplinary cooperation. Clearly stated by Simkin, the Conference worked on the premise that conservation and science in the Galápagos cannot be separated. With respect to the status of plant ecology, it was characterized by Charles Rick as "one of tremendous deficiencies." The Conference recommended a range of priority research subjects in botany, including vegetation mapping and quantitative sampling, plant–animal interrelationships, phytogeography, reproductive ecology, and population structure. In terms of conservation needs, the priority research subjects identified were detailed autecologies, long-term population dynamics and/or monitoring, and the environmental effects of introduced plants and animals.

These concerns and recommendations were reflected clearly in the 1974 Management Plan for the Galápagos National Park (PNUD, Unesco, FAO, 1974). One of the most important objectives of the maintenance and protection of indigenous ecosystems in the Park is to make possible scientific research that can only be carried out in the Galápagos Islands. A number of studies were identified as indispensable for the development of management techniques:

Monitoring of the biological communities by means of plant and animal censuses using standardized quadrats and transects.

Research on population size and dynamics of certain endangered species.

Detailed studies of the population dynamics of introduced organisms and the development and improvement of eradication methods for them.

Environmental checks for contaminants originating outside the archipelago.

Synoptic study of the flora and fauna of offshore zones.

Studies of tourism impact.

Assessment of water resources and volcanic hazards.

During the 1970s, a steadily increasing number of research projects were carried out by visiting scientists and by resident scientists of the Charles Darwin Research Station (CDRS). Within the work program of the CDRS, emphasis was placed on research thought to be of immediate use for conservation management, and visiting researchers often conducted high priority conservation-related research. A brief perusal of the 1979 annual report of the CDRS reveals that studies were under way in the fields of monitoring, population dynamics, marine biology, and so forth. In 1980 the Charles Darwin Foundation made a reassessment of the situation at a seminar in Quito (CDF, 1980). Very clear priorities were formulated for research applied to the protection of natural resources and for basic research. Comparing these with the recommendations made by the 1972 Galápagos Science Conference and the identified priorities of the 1974 Management Plan reveals some important facts:

FIGURE 1. —A. *Scalesia microcephala*, Fernandina Island. Flower heads about 8 mm broad.—B. *Scalesia affinis* subsp. *gummifera*, Isabela Island. Flower heads about 25 mm broad. The endemic genus *Scalesia* (Asteraceae) comprises 21 taxa of trees and shrubs, which are conspicuous and characteristic elements in the Galápagos vegetation.

1. The conceptual perception of research and conservation in the Galápagos is changing with the focus shifting toward the question of managing the resources in a sustainable way, e.g., in terms of tourism and carrying capacity of the ecosystems and in terms of involving the local population in the overall development of the park.
2. The problems caused by introduced plants and the breakdown of interisland isolation was recognized to be of major concern.
3. With respect to botanical studies, particularly in ecology, several gaps were still evident.

THE PRESENT SITUATION

An up-to-date information on the present status of research and conservation in the Galápagos is presented in two recent volumes: *Key Environments. Galápagos*, 1984, edited by R. Perry, and *El Niño in the Galápagos Islands: the 1982–83 Event*, 1985, edited by Robinson & del Pino. In the *Key Environments* volume, many research areas are presented in a comprehensive fashion, and Bowman described some of the major contributions to science from the Galápagos. In the *El Niño* volume, the ecological effects of the extraordinary heavy El Niño phenomenon are dealt with from several points of view, altogether forming a unique lesson for conservation.

TABLE 1. Summary of botanical research needs of relevance to management in the Galápagos.

Topic	Management relevance	Comments
1. Qualitative inventory	Reserve selection. Identification of management objectives. Information service.	Generally low priority for management authority apart from selection phase.
2. Quantitative inventory	Information. Planning and reserve management. Monitoring.	Should be part of routine monitoring. Of high priority for dealing with endangered plants and vegetation types (e.g., endemics).
3. Vegetation mapping	Monitoring. Habitat management. Determining management priorities.	Some form of vegetation map a priority for parts of the archipelago (e.g., inhabited islands).
4. Succession studies	Determining needs for habitat management.	Of particular importance in view of volcanic habitats. Long-term monitoring highly relevant (e.g., Sierra Negra).
5. Synecological studies	Planning suitable management of species and habitats.	Long-term monitoring of relevance (e.g., humid forests and *Sphagnum* bogs).
6. Autecological studies	Improving management or protection of special species. Habitat requirements.	Of high priority for conserving threatened species (e.g., *Scalesia* species).
7. Special problem studies	Solving emergency or special management problems.	Very high priority (e.g., invasive alien species and utilization of exotic trees).
8. Consequences of management	Evaluating management effectiveness. Planning management action.	A continuous priority (e.g., assessing control programs aimed at introduced species).
9. Socioeconomic studies	Relations with surrounding lands. Economic justification. Visitor use.	High priority.

The botanical research treated in these volumes demonstrates that much has happened since 1971. It is also true that results of numerous botanical research projects are published or reported upon elsewhere, for example in the yearbooks of the CDRS from 1980 onward. The following areas of botanical research have been the subject of investigations in the Galápagos during the last 15 years or so (this list is not exhaustive): taxonomy, biography and evolution of plants, historical ecology, vegetation mapping, descriptive vegetation ecology, succession, regeneration of vegetation, effects of exotic herbivores, spread of introduced plants, pollination and dispersal of plants, plant–animal relationships, and population biology of certain species (see, for example, Fig. 1).

RESEARCH PRIORITIES IN RELATION TO CONSERVATION

From the brief outline above it is obvious that to compile the existing data on Galápagos flora and vegetation and its dynamics is no small task, considering the amount and variety of investigations that have been carried out during the last 15 years. However, a general framework for dealing with such research in relation to management has been suggested by MacKinnon et al. (1986)—a framework that may be modified to exemplify the Galápagos situation. In their treatment of how to plan research programs for protected areas, they presented a table, in which different kinds of research needs are annotated with respect to management relevance, outside execution, staff execution, sponsorship, and priority rank. Table 1 is a shortened and modified version as I see it applies to the Galápagos situation, focusing on the botanical aspects of relevance to management.

Concluding Remarks

The purpose of the Workshop on Botanical Research and Management in the Galápagos Islands, April 1987, is very practical. The aim is not merely to discuss scientific papers, but rather also to assess how botanical research can contribute to the practical conservation of the unique flora and vegetation of the Galápagos. In other words, guidelines for botanical research and management in the Galápagos should be extracted to provide the Ecuadorian authorities with informed considerations on which sound management policies may be formulated and decisions taken.

Based on my experience in the Galápagos since 1971 and in international conservation, I propose that it is high time that plant and vegetation conservation in the Galápagos Islands is given very high priority. Much of the archipelago is still pristine, but unless action is taken now, the islands may suffer the fate of so many other oceanic islands of the world: increasing loss of diversity and loss of unique natural resources. The signs are beginning to show in the Galápagos as indicated, for example, by the growing problem of invasive exotic plants, so there is an urgent need to spell out the problems in accurate detail if adequate measures are to be taken.

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THREATENED PLANTS IN GALAPAGOS

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ABSTRACT

A survey shows that 144 of the 604 Galápagos species of higher plants may be listed as rare. All but 30 of these rare plants are affected by human activities. Among endemics, 31% are rare; among nonendemic natives, 20% are rare. Land use comprises the worst risk to the rare species. Attention is called to plant species protection.

The Galápagos Islands have often been called a living laboratory of evolution. Due to the successes of the joint efforts of CDRS, SPNG, and their many private, institutional, and official collaborators, the management of the Galápagos's natural treasures has become a showcase of conservation.

As in many other reserves, the plant world has received attention mainly as the scene for the activities of the spectacular animals, or as the source of color and fragrance of the landscape. Great achievements have been accomplished in Galápagos botany, largely as descriptive works or studies closely connected to the animal populations. The Galápagos flora and vegetation have been well documented by the works of Wiggins & Porter (1971), van der Werff (1978), and Hamann (1981), and by numerous more narrowly focused studies, but the state and fate of the Galápagos plants and vegetation have not yet been dealt with in detail. Such work is essential for rational conservation measures directed to the preservation of plant species and plant communities.

The aim of the present paper is to establish a factual account on present and future status of Galápagos plants. The data have been gathered through my 13 years of acquaintance with the Galápagos environment. The focus will be on the plants that have suffered during this period.

There is a clear distinction between the plant species approach and the vegetation approach. The conservation strategy deals with both: it is prohibited to bring species from island to island, and the ecosystems (including vegetation) should be preserved. For the protection of animals, most emphasis has been on the species approach, whereas for the plants, most weight has been put on vegetation protection.

THREATENED PLANTS

One of the reasons that plant species protection has played a minor role is that we still lack one of the fundamentals for species preservation: accurate distribution maps. For the Galápagos, where species protection aims at the maintenance of intra-archipelago distribution for each taxon, maps are essential. The pteridophytes have been mapped so far, and a checklist with rough distribution indications has recently been published (Lawesson et al., 1987).

Several authors have pointed out particular plants or plant groups as threatened (Eliasson, 1982; Hamann, 1984; van der Werff, 1982; Lawesson, this volume). Two detailed treatments are under way: Porter & Lawesson evaluate the flora from IUCN category criteria (summarized by Lawesson, this volume), and I (Adsersen, 1989) have studied the status and prospects of the plants that may be termed "rare," because they have been collected infrequently or occur in areas where human or exogenous impact threatens the plants or the vegetation in which they grow. The plants defined by

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FIGURE 1. *Passiflora colinvauxii*, an endemic passionflower, characteristic for the evergreen forests of Santa Cruz. (Photo taken by J. E. Lawesson.)

these criteria are roughly those assigned to all IUCN categories other than "nt" (not threatened); they may therefore as well be designated "threatened." The main trends of Galápagos plants defined in this way as threatened are presented here.

Galápagos may be considered as home to 604 indigenous species and subspecies. Of these, 226 are endemics (Fig. 1)—the rest are termed (nonendemic) natives. Of these 604 indigenous plants, 144 may be designated threatened. They are unevenly distributed among native and endemic plants; as shown in the table, endemics are 1.54 times more likely to be threatened than nonendemic natives.

An attempt was made for each of the threatened plants to describe the distribution pattern, stability of populations, and the threats separately for each of the major islands. In some cases it was not possible to identify threats other than the general risk of being low in numbers. It proved that all but 30 of the threatened plants were affected by human activities in Galápagos—22 natives and 8 endemics, rendering 71% of the threatened (nonendemic) native and 88% of the threatened endemic plants at risk somewhere in the archipelago by the activities of humans. Land use for agriculture, urbanization, sand and gravel excavation, and tourism exhibits the most serious menace: executed or planned activities threaten 77 plants (13% of the entire flora, and 54% of the threatened plants). Roughly half of the threatened endemics and 57% of the threatened (nonendemic) natives are jeopardized by land use.

Introduced animals are a well-known problem. Fifty-eight plants are immediately threatened by introduced grazers, worst so the endemics: 43 endemics, or 61% (19% of all endemics) are losing terrain significantly, whereas grazing only is a menace to 20% of the threatened (nonendemic) natives. Grazing obviously favors native *and* alien plants. Introduced plants constitute grave problems only on inhabited islands; therefore, only 28 plants are threatened (so far) by introduced plants. Again the threatened endemics outnumber the threatened (nonendemic) natives: 20 vs. 8. This may be interpreted as a reflection of less resistance to competition in plants that evolved in the rather species-poor Galápagos environment.

TABLE 1. Endemism and rarity in the Galápagos flora. Data from Adsersen (1989).

	Natives	Endemics	Endemics/ natives
Total species	378	226	0.60
Rare species	75	69	0.92
Rare/total	0.20	0.31	1.54

Fire may be considered a natural risk in arid, volcanic environments such as Galápagos. However, human activities increase the fire risk considerably. The effects of great fires may be illustrated by the 1985 fire on Sierra Negra. One-third of the largest coherent vegetation area in the islands burned, and at least 18 threatened species had major parts of their populations on Sierra Negra destroyed. This constitutes 12% of the threatened species in the archipelago. The number is possibly much higher, since Sierra Negra is poorly investigated floristically.

Twelve species are considered probably extinct. Six of these probably disappeared after 1960, and there is no doubt that more will follow during the next decades. One vanished when the Fernandina caldera collapsed in 1968—one was probably burned off on Sierra Negra. Land use accounts probably for six extinctions and introduced animals for three. Hence most extinctions are directly or indirectly connected with human activities. Seen from the positive side, this means that we may reduce the extinction rate by managing these activities.

It would take too much space to consider which species are most vulnerable to the panoply of perils, but a few general aspects can be outlined. There seems to be most danger to arboreal or shrubby endemics. The threatened plant list comprises 12 taxa of *Scalesia*, three of *Darwiniothamnus*, and two of *Lecocarpus*. These may well be compared in uniqueness to the tortoises and iguanas. The list also includes some former important or even predominant members of their plant communities. *Scalesia pedunculata*, *Miconia robinsoniana*, and *Cyathea weatherbyana* are good examples. There is no doubt that it is time to start emergency aid, such as fenced areas and in many cases to initiate captive breeding or ex situ conservation.

CONCLUSION

Conservation of plant species and plant communities has always been an integral part of the activities of CDRS and SPNG. If this part has played a minor role, it is partly a reflection of the fact that it is easier to raise interest and money for the protection of animals than for the protection of plants, and partly because the plight of the animals was recognized earlier. However, there is need for immediate actions in order to avoid impoverishment of the Galápagos flora. Among these actions, which should be aimed directly toward plant protection, are the following:

1. Confirmation of present national park limits in order to resist demands for more ground for agriculture, urbanization, and tourism.
2. Intensification of eradication programs against introduced plants and animals.
3. Extended control and guidance on import of plants for cultivation.
4. Emergency aid to endangered species in the forms of gene bank exclosures and cultivation in safe habitats within or outside the islands.
5. Monitoring rare plants.

These activities should be supplemented by research studies of the taxonomy, evolution, distribution, and life histories of Galápagos plants, and scientific investigations on structure, function, and dynamics of Galápagos vegetation.

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ALIEN PLANTS IN THE GALAPAGOS ISLANDS, A SUMMARY[1]

Jonas E. Lawesson[2]

ABSTRACT

Plants introduced in the Galápagos as of spring 1987 are listed. Separately listed are highly invasive naturalized species with date of introduction and approximate area invaded. These are discussed briefly.

The number of plant species introduced to Galápagos by humans has been rapidly increasing during recent years, presumably due to the growing human population and its ornamental (Fig. 1) and cultivated plants (Fig. 2). With the large flow of people and cargo from the mainland to Galápagos, the accidental introduction of alien organisms must play an increasingly important role. Alien species increased from about 77 in 1971 (Wiggins & Porter, 1971) to about 260 species reported in this paper. Thus, over 10 alien plant species have been introduced to Galápagos per year since 1970. The complete list of known alien species is given in Table 1. The nomenclature is according to Lawesson et al. (1987). The alien species are mainly found on the four inhabited islands: Santa Cruz (197 species), Floreana (89 species), San Cristóbal (110 species), and Isabela on Sierra Negra (68 species) with high concentrations of species in the mesic, agricultural areas at higher elevations (see Fig. 3). From there, several species have naturalized in National Park areas (Table 1, marked with asterisk).

Although most species have not yet altered the ecological equilibrium significantly, such species as *Psidium guajava, Lantana camara, Eugenia jambos, Cinchona succirubra, Pennisetum purpureum,* and *Rubus* sp. have invaded large areas, forming monospecific stands or altering vegetation types. The invasion is still going on, and large areas with unique vegetation, such as the evergreen *Scalesia* forests and *Miconia* shrub, are headed toward extinction in very few years. The most invasive alien plants are listed in Table 2, which gives their distribution in Galápagos and the approximate minimum area invaded.

Very few resources have been available to initiate control of the alien species. A few, small-scale experiments with herbicides have been undertaken in Santa Cruz to find appropriate agents to control *Psidium guajava* and *Cinchona*. One may ask, however, if this is at all possible, when more than 40,000 ha are covered by *Psidium guajava* thickets and some 4,000 ha by *Cinchona*. With the very limited financial resources allocated annually, results have been lean. Systematic and effective control must rely on a much larger and reasonably secure economic foundation, and an approach using biological, chemical, and physical solutions. Efforts to prevent further introductions and to eradicate undesired species by the Charles Darwin Research Station and the Galápagos National Park Service must be backed up by local and national authorities.

It should be prohibited by law to cultivate undesired species, which should be designated "noxious weeds." There is wide experience with this legal measure available from other parts of the world. To coordinate the efforts for control of introduced plants, a new unit in the Charles

[1]Practical and economic support given by the Charles Darwin Research Station and the Galápagos National Park Service is gratefully acknowledged. Anni Sloth skillfully prepared the photographs. The Danish Natural Science Research Council sponsored the fieldwork (grant numbers 11-5471, 11-5663, and 11-6288). Contribution No. 133 of the AAU Ecuador project.

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FIGURE 1. *Lantana camara*, one of the most aggressive alien plants introduced to Galápagos.

FIGURE 2. Large areas on the populated islands have been covered by the introduced tree *Psidium guajava*.

TABLE 1. Introduced plants in Galápagos, spring 1987. (* indicates naturalized species in National Park areas.)

GYMNOSPERMS

Cupressaceae: *Cupressus macrocarpa*

Pinaceae: *Pinus radiata*

ANGIOSPERMS

DICOTYLEDONS

Acanthaceae: *Elytraria imbricata*

Amaranthaceae: *Achyranthes aspera, Alternanthera lanceolata*, A. sessilis*, Amaranthus dubius*, A. gracilis*, A. lividus*, A. quitensis*, A. spinosus*

Anacardiaceae: *Mangifera indica, Schinus molle, Spondias purpurea*

Annonaceae: *Annona cherimola, A. muricata*

Apocynaceae: *Nerium oleander*

Asclepiadaceae: *Asclepias curassavica**

Balsaminaceae: *Impatiens balsamina**

Begoniaceae: *Begonia rex*

Bignoniaceae: *Crescentia cujete, Spathodea campanulata*

Bixaceae: *Bixa orellana**

Bombacaceae: *Ceiba pentandra, Matisia cordata, Ochroma pyramidale*

Boraginaceae: *Cordia alliodora**

Capparaceae: *Cleome viscosa**

Caprifoliaceae: *Sambucus mexicana*

Caricaceae: *Carica papaya**

Caryophyllaceae: *Stellaria media**

Casuarinaceae: *Casuarina equisetifolia*

Chenopodiaceae: *Beta vulgaris, Chenopodium ambrosioides*, C. murale, Spinacia oleracea*

Combretaceae: *Terminalia catappa*

Compositae: *Adenostemma lav, Ambrosia artemisiifolia*, Bidens cynapiifolia*, Chrysanthemum* sp., *Conyza canadensis*, Dahlia variabilis, Erechtites hieracifolia* var. *cacaloides*, Flaveria bidentis*, Fleischmannia pratensis*, Galinsoga caracassana*, G. urticifolia*, Jungia hirsuta*, Lactuca sativa, Porophyllum ruderale*, Pseudelephantopus spicatus*, P. spiralis*, Sonchus oleraceus*, Spilanthes acmella*, Synedrella nodiflora*, Tagetes erecta, Tridax procumbens*

Convolvulaceae: *Ipomoea batatas*, I. nil*, I. pulchella*, Merremia umbellata**

Crassulaceae: *Kalanchoë pinnata**

Cruciferae: *Brassica campestris*, Coronopus didymus**

Cucurbitaceae: *Cucumis dipsaceus*, C. maxima, C. melo, C. pepo, C. sativus, Momordica charantia**

Dilleniaceae: *Dillenia indica*

Elaeocarpaceae: *Muntigia calabura*

Euphorbiaceae: *Chamaesyce hirta*, C. lasiocarpa*, C. ophtalmica*, Codiaeum variegatum, Euphorbia lactea, E. millii, E. pulcherrima, Jatropha curcas, Manihot esculenta, Phyllanthus acidus, Ricinus communis**

Geraniaceae: *Pelargonium* sp.

Juglandaceae: *Juglans neotropica*

Labiatae: *Hyptis mutabilis*, H. rhomboidea*, H. sidifolia*, Mentha piperita*, Ocimum micranthum, Origanum vulgare, Stachys agraria*, S. arvensis*

Lauraceae: *Persea americana**

Leguminosae: *Acacia nilotica, Albizia guachepele, Arachis hypogea, Bauhinia* cf. *aculeata*, B. variegata, Canavalia dictyota*, Cassia bicapsularis*, C. hirsuta*, C. tora*, Crotalaria retusa*, Delonix regia, Dioclea reflexa, Glycine max, Inga edulis, I. schimpffii, Lablab purpureus, Lathyrus* sp., *Mimosa acantholoba, M. pigra, Mucuna rostrata, Phaseolus lathyroides, P. vulgaris, Pisum sativum, Schizolobium* sp., *Tamarindus indica, Zornia curvata*, Z. piurensis**

Lythraceae: *Cuphea carthagensis*, C. racemosa**

Malpighiaceae: *Byrsonima* sp.

Malvaceae: *Abelmoschus manihot, Anoda acerifolia*, Hibiscus diversifolius*, H. rosa-sinensis, Malachra alceifolia*, Malva alcea, M. parviflora, Malvastrum americanum, M. coromandelianum*, M. scoparium, Sida acuta*, S. ciliaris*, S. glutinosa, S. paniculata*, S. rhombifolia**

TABLE 1. Continued.

Meliaceae: *Cedrela odorata**, *Melia azedarach**, *Swietenia macrophylla*
Moraceae: *Ficus carica*
Myrtaceae: *Eugenia jambos**, *E. malacacensis**, *Psidium guajava**, *Eucalyptus maculata* var. *citriodora*
Nyctaginaceae: *Boerhaavia coccinea*, *Bougainvillea spectabilis*, *Mirabilis jalapa*
Oxalidaceae: *Oxalis corniculata**, *O. corymbosa**
Papaveraceae: *Argemone mexicana**
Passifloraceae: *Passiflora edulis**, *P. ligularis**, *P. quadrangularis**
Phytolaccaceae: *Rivina humilis**
Piperaceae: *Pothomorphe peltata**
Plantaginaceae: *Plantago major**
Polemoniaceae: *Phlox* sp.*
Polygonaceae: *Antigonon leptopus*, *Rumex crispus**, *Triplaris cumingiana*
Primulaceae: *Anagallis arvensis**
Punicaceae: *Punica granatum*
Rhamnaceae: *Gouania polygama*
Rosaceae: *Eriobotrya japonica*, *Malus pumila*, *Prunus* sp., *Rubus* sp.*
Rubiaceae: *Cinchona succirubra**, *Coffea arabica*, *Oldenlandia corymbosa*, *Spermacoce confusa*
Rutaceae: *Citrus aurantiifolia*, *C. aurantium*, *C. limetta*, *C. limon**, *C. medica*, *C. paradici*, *C. reticulata*, *C. sinensis**
Scrophulariaceae: *Russelia equisetiformis*, *Stemodia verticillata*, *Veronica montana**
Solanaceae: *Browallia americana**, *Brugmansia candida**, *Capsicum annuum**, *C. pendulum*, *Cyphomandra betacea*, *Datura innoxia**, *D. stramonium* var. *stramonium*/var. *tatula**, *Lycopersicum esculentum*, *Nicandra physalodes**, *Nicotiana tabacum**, *Physalis peruviana*, *Solanum melongena*, *S. tuberosum*
Sterculiaceae: *Guazuma ulmifolia*
Tropaeolaceae: *Tropaeolum majus*
Umbelliferae: *Apium graveolens**, *Coriandrum sativum*, *Daucus carota*, *Petroselinum crispum*, *Peucedanum sativum*
Urticaceae: *Pilea microphylla*, *Urera caracasana**
Verbenaceae: *Lantana camara**, *Lippia reptans**, *Priva lappulacea**, *Stachytarpheta cayennensis**, *Tectona grandis*, *Verbena brasiliensis**
Vitaceae: *Vitis vinifera*

MONOCOTYLEDONS

Agavaceae: *Furcraea cubensis**
Araceae: *Colocasia esculenta*
Bromeliaceae: *Ananas sativus*
Cannaceae: *Canna lutea**
Commelinaceae: *Zebrina pendula**
Cyperaceae: *Cyperus alternifolius*, *C. compressus*, *C. odoratus*, *C. rotundus*, *Rhynchospora nervosa* subsp. *nervosa**
Gramineae: *Axonopus compressus**, *Bambusa guadua*, *Coix lacrima-jobi*, *Cynodon dactylon**, *Dactyloctenium aegypticum**, *Digitaria ciliaris**, *D. decumbens**, *Echinochloa colonum**, *Eleusine indica**, *Eragrostis pilosa**, *Melinus minutiflora**, *Panicum maximum**, *P. muticum**, *Paspalum conjugatum**, *Pennisetum purpureum**, *Saccharum officinarum*, *Setaria vulpiseta**, *Zea mays*
Liliaceae: *Allium ampeloprasum*, *A. cepa*, *A. sativum*, *Aloe barbadensis*, *Asparagus officinalis*, *Sansevieria trifasciata*
Musaceae: *Musa acuminata*, *M.* ×*paradisiaca*, *M. sapientum* var. *champa*
Palmae: *Cocos nucifera*

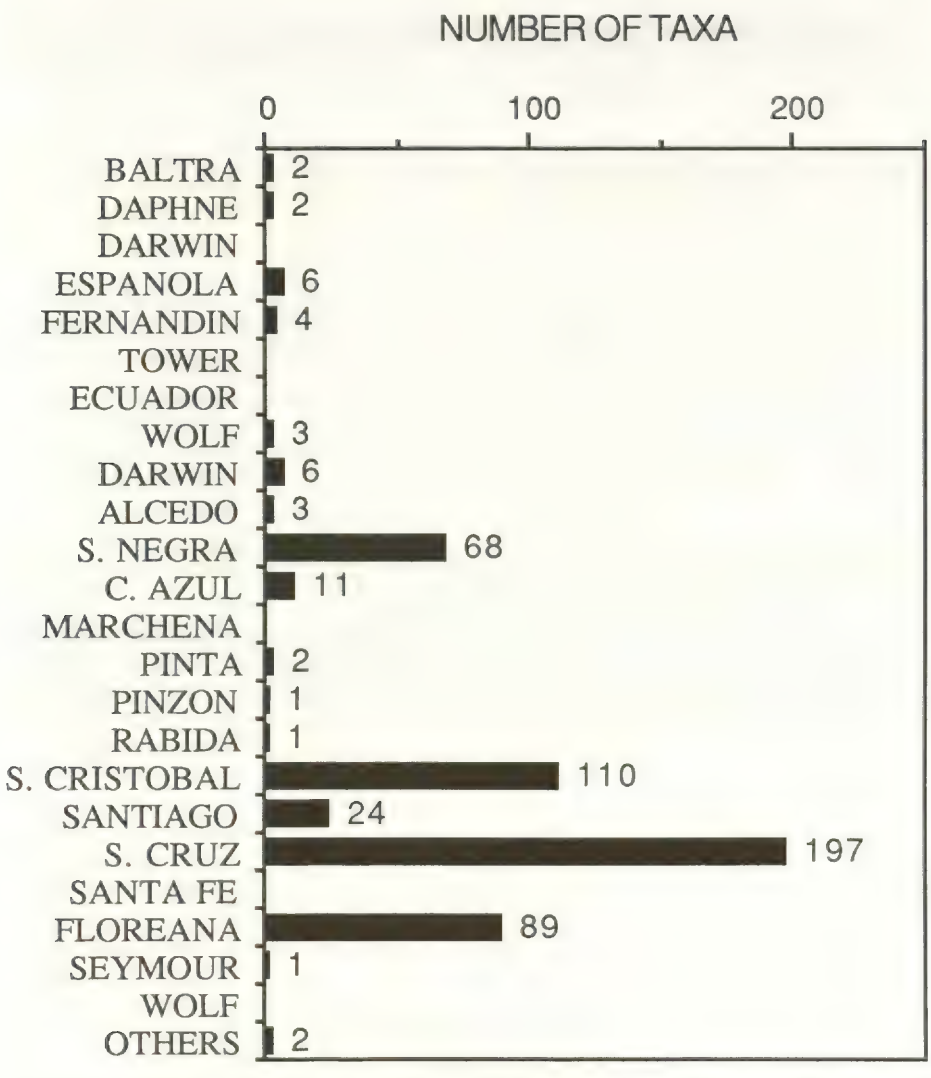

FIGURE 3. Introduced plants in Galápagos, as found on the different islands, or for Isabela the different volcanoes (Ecuador, Wolf, Darwin, Alcedo, Sierra Negra, and Cerro Azul).

TABLE 2. Some highly invasive naturalized plant species in Galápagos, including date of first introduction and approximate area invaded per island (SC = Santa Cruz, F = Floreana, I = Isabela, C = San Cristóbal). + indicates presence.

Family and species	Dates of introduction	Island distribution/ha			
		SC	F	I	C
Myrtaceae					
Psidium guajava	ca. 1858	100	8,000	20,000	12,000
Eugenia jambos	?	1	1	5	50
Verbenaceae					
Lantana camara	1940	1	2,000		1
Rubiaceae					
Cinchona succirubra	1946	4,000			
Agavaceae					
Furcraea cubensis	?	10	1	10	10
Crassulaceae					
Kalanchoë pinnata	?	+	50	10	10
Rosaceae					
Rubus sp.	1983	1			100
Poaceae					
Pennisetum purpureum	?	5,000	150	?	?

Darwin Research Station is suggested, analogous to the Department on Introduced Mammals. Only with such an entity can the necessary attention be given to the complex problems caused by introduced plants. Alien plants in Galápagos are further discussed in this volume by de Vries & Tupiza, Gordillo, and Lawesson & Ortiz.

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SOME UNIQUE ECOLOGICAL ASPECTS OF OCEANIC ISLAND ECOSYSTEMS[1]

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ABSTRACT

Island biota and ecosystems are highly vulnerable to disturbances associated with human activities, the most serious of which are the introduction and release of grazing mammals and pyrophytic grasses. We discuss five of the most aggressive alien plants that caused massive displacement of native biota in Hawaii. Native species that evolved in isolated environments are not inherently weak or always poor competitors. They often cope well with natural (nonanthropogenic) disturbances and are commonly the better competitors in harsh environments. Their survival strategies work well under conditions that contain a prevalence of the original evolutionary stresses and ecological conditions. The hope of island conservation management lies in maintaining and restoring some of these conditions.

The Hawaiian and Galápagos archipelagos have many similarities. The most striking include their isolation from continents, comparable land areas, high biological endemism, and active volcanism. Simkin (1984) stated that during a recent 15-year period, Hawaii, the most active site of volcanism in the world, was active for 10 years, followed by the Galápagos and Reunion (in the Indian Ocean) with activities for seven years each. Our paper discusses some unique ecological problems of islands primarily from the perspective of work on one of the most intensively studied (along with Santa Cruz of the Galápagos) oceanic islands of the world—the island of Hawaii, the largest and youngest of the Hawaiian Islands.

The area of Hawaii Volcanoes National Park and vicinity was selected as the site for island studies as part of the contribution of the United States to the International Biological Program (IBP) 1971–1976. Because of extensive relatively undisturbed ecosystems, relatively secure long-term research sites within the national park (although volcanism tends to reduce the security), and excellent logistical facilities available at the Research Center of Hawaii Volcanoes National Park, the island of Hawaii has been used continually by researchers from the University of Hawaii, the B. P. Bishop Museum, and other research institutions.

One of the questions asked during the IBP work was, "What is unique about the ecology of island ecosystems?" (Mueller-Dombois et al., 1981). In this paper, we attempt to answer this question, at least in part, from a Hawaiian perspective with the aim of stimulating exploration of similarities and differences among oceanic island groups of the world.

VULNERABILITY VERSUS RESILIENCE OF ISLAND BIOTA

Many travelers to islands, including the well-traveled 19th-century naturalists Darwin (1859), Hooker (1867), and Wallace (1880), have been impressed with the susceptibility of islands to invasions of continental plants and animals and have been pessimistic about the survival of island biota. Darwin (1859) stated: "He who admits the doctrine of the creation of each separate species will have to admit that a sufficient number of the best adapted plants and animals were not created

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for oceanic islands; for man has unintentionally stocked them far more perfectly than did nature." Books by Degener (1930), Zimmerman (1948), Elton (1958), Carlquist (1965, 1974, 1980), and others have elaborated on and supported this view, particularly in regard to the Hawaiian Islands. In recent years, the need for active management to protect island ecosystems from the worst invaders (especially feral mammals) is becoming well accepted in national parks and other reserves of Hawaii (e.g., Stone & Loope, 1987).

Small population size and small distributional area are obvious reasons for the vulnerability of island species to extinction. In addition, oceanic islands have been predisposed to vulnerability to certain types of human-related invasions because of long isolation from the continual challenge of some of the forces that shape continental organisms—including such forces as browsing and trampling by herbivorous mammals, ant predation, virulent disease, and frequent and intense fires (Loope & Mueller-Dombois, 1989).

Browsing and trampling by feral and domestic goats, pigs, cattle, sheep, and deer are recognized by most ecologists in Hawaii as comprising the single most destructive force in Hawaiian ecosystems at present. Huge tracts of forest have been converted to pastureland simply through the persistent action of these mammals. Survival of native forest in many of Hawaii's State Forest reserves is threatened currently by feral ungulates. In Hawaii, grazing and browsing effects are magnified beyond the levels seen in continental ecosystems because of the absence of natural controls, and an associated acceleration of concentration effects.

The Hawaiian Islands lack endemic ants, and the native fauna has not developed adaptations against ant predation. About 40 species of alien ants have invaded the islands, with 34 species recorded for the island of Hawaii (Huddleston & Fluker, 1968). Alien ants, especially *Pheidole megacephala*, are believed to have decimated the native arthropod biota below 600 m elevation (Zimmerman, 1948). Other ant species, especially *Iridomyrmex humilis*, threaten the arthropod biota at higher elevations (Medeiros et al., 1986).

Introduced diseases, particularly avian malaria and avian pox, are believed to have played a major role in depleting the endemic Hawaiian bird fauna (Scott et al., 1986; van Riper et al., 1986). These diseases and their vectors were introduced in the past century. Most Hawaiian drepanids (honeycreepers) are thought to be limited in distribution and abundance due to disease.

Fire does not appear to have been important in most native ecosystems of Hawaii, and most native plants of the Hawaiian Islands lack adaptations to fire (Mueller-Dombois, 1981a). Lightning is relatively uncommon on islands because their small land mass is not conducive to convective buildup of thunderheads. Fires in modern Hawaii, carried mainly by introduced grasses, are generally highly destructive to native plant species. Opportunistic alien plant species spread rapidly following fire or other disturbance.

We emphasize that by no means all island species exhibit reduced aggressiveness and increased vulnerability to extinction. For example, the native fern *Dicranopteris linearis* aggressively colonizes disturbed areas, in some cases displacing aggressive alien woody plants. Native plants exhibit particularly marked competitive superiority over aggressive alien species in extreme habitats, such as on new lava flows (Smathers & Mueller-Dombois, 1974), on soils with aluminum toxicity (Gerrish & Mueller-Dombois, 1980), and in montane bogs (Canfield, 1986), unless specifically adapted aliens are introduced. *Metrosideros polymorpha*, one of the more aggressive native colonizers and the dominant tree in many Hawaiian forests, possesses a number of races, some of which are successful colonizers of recent lava flows, others are better adapted to older soils, and still others to bogs (Stemmermann, 1983). Removal of the influence of feral ungulates enhances the tenaciousness of native species. For example, the endemic leguminous vine *Canavalia kauensis* was first collected from a newly constructed exclosure in Hawaii Volcanoes National Park in 1970. Within two years, it temporarily comprised 46% of the vegetation cover in the area and has since fluctuated between 40% and 2% (Mueller-Dombois, 1981b). Studies of vegetation response within fenced exclosures have shown that at least partial recovery of native vegetation occurs in most instances after alien ungulates are removed (Loope & Scowcroft, 1985).

Massive Invasions by Alien Plant Species

Vulnerability of Hawaiian ecosystems to disturbance by feral animals aided the establishment of many alien plant species. Over 4,600 vascular species have been introduced to the Hawaiian Islands (St. John, 1973), and 10–15% of them maintain populations in natural or seminatural environments. Smith (1985) considered 86 species to be particularly troublesome pests in nonagricultural areas. Only one or a few very aggressive alien plant species may disrupt an otherwise nearly natural ecosystem, especially when aided by disturbances caused by feral animals. We discuss five of the most troublesome flowering plant invaders of the island of Hawaii below. All five are already abundant in Hawaii Volcanoes National Park.

Passiflora mollissima (banana poka), a vine, was introduced to the Hawaiian Islands as an ornamental in the early 1900s. It is uncommon in its native habitat in the Andes where it is eaten by numerous species of insects. Lacking these predators in Hawaii, it has spread to become established in 500 km^2 of native forest on the islands of Hawaii and Kauai. In some areas, it fills forest light gaps and fatally engulfs tree saplings under a blanket of foliage. It occupies elevations from 610 to 1,525 m and thrives where mean annual precipitation is between 500 and 5,000 mm. Feral pigs are its primary dispersal agent, but alien birds spread the *Passiflora* as well (Warshauer et al., 1983). A cooperative effort is under way by several federal and state agencies to screen organisms from *P. mollissima*'s native habitat in South America for possible introduction to Hawaii as biocontrol agents (Smith, this volume).

Psidium cattleianum (strawberry guava), from the Neotropics, is a shrub, small tree, or large tree, depending on density of stocking and habitat conditions. It establishes dense stands in rainforests from primarily pig-dispersed seed (Diong, 1983) and tends to displace native species. Its elevational range is approximately from 150 to 1,300 m (Smith, 1985). This species is more shade tolerant than *Metrosideros polymorpha* and other native trees, and it forms nearly impenetrable thickets. Strawberry guava potentially threatens numerous low- to mid-elevation rainforest plant species with extirpation through displacement of reproduction. At one site on Maui, *P. cattleianum* occupies over 75% of the understory and rises into the canopy, attaining diameters of 30 cm and heights of 18 m (J. Jacobi, pers. comm.).

Myrica faya (faya tree), from the Canary Islands, Madeira, and the Azores, is one of the worst invaders in mesic and wet habitats (at 300–1,700 m elevation) of Hawaii Volcanoes National Park, where it has increased 20-fold over an eight-year period (Whiteaker & Gardner, 1986). It typically invades developing *Metrosideros* forest on new volcanic ash deposits but does not establish on lava flows. *Myrica* is killed aboveground by fire, but resprouts from its base (Smith, 1985). This tree fixes large quantities of nitrogen in symbiotic association with *Frankia* in root nodules and has great potential for massive alteration of nitrogen-poor ecosystems (Vitousek et al., 1987). It is often interspersed with *Andropogon virginicus*.

Andropogon virginicus is a tall, perennial bunchgrass of dry, mesic, and wet sites that has invaded vast areas in the Hawaiian Islands and is particularly abundant at low and middle elevations in Hawaii Volcanoes National Park. Its cover increases dramatically with each fire (Smith, 1985). Fire intensities and area burned have increased in areas where it occurs. Native to the southeastern United States, this grass maintains its temperate-zone phenology in the Hawaiian Islands, growing during the dry season and remaining inactive, with much-reduced transpiration while strongly retarding evaporation from the soil, during the wet season (Mueller-Dombois, 1973). A common result is development of swampy, *Andropogon*-covered sites in areas of high rainfall, and an increase in runoff and erosion.

Leucaena leucocephala is a fast-growing alien leguminous tree that spreads rapidly in the arid lowlands of the Hawaiian Islands when freed from browsing pressure. Removal of feral goats from Hawaii Volcanoes National Park has hastened its spread there. It reproduces abundantly by seed and recovers rapidly from fire through basal sprouting (Smith, 1985). Although highly regarded as a valuable, nitrogen-fixing forage plant for tropical countries of the world (Anonymous, 1977), it threatens recovery of native lowland vegetation in Hawaii Volcanoes National Park. Recently, *Leucaena* has undergone stand-level dieback in many areas of Oahu, Kauai, and Maui; the effects on vegetation change are not yet known.

Community Structure on Islands and Its Consequences

Not only do islands generally have fewer species than comparable mainland communities, but one or a few species are often overwhelmingly dominant in island forests. Two such dominants in Hawaiian communities are the endemic trees ʻōhiʻa lehua (*Metrosideros polymorpha*) and koa (*Acacia koa*). The canopies of most of the relatively intact forests remaining in the Hawaiian Islands are dominated by one of these species. Over 80% of the relatively intact forests are dominated by *Metrosideros polymorpha*. *Acacia koa* is often associated as a second major canopy species in *Metrosideros* forest at its upper and lower elevational limit (ca. 550 m and 1,650 m) on the island of Hawaii. *Metrosideros* rainforest is further characterized by a number of associated subcanopy species belonging to the Aquifoliaceae, Araliaceae, Euphorbiaceae, Gesneriaceae, Lobeliaceae, Myrsinaceae, Rubiaceae, Rutaceae, Thymeliaceae, and Urticaceae. Tree ferns of the genus *Cibotium* and herbaceous ferns are important in the understory.

Succession on a new lava flow in a rainforest climate on the island of Hawaii takes about 400 years for establishment of mature rainforest (Atkinson, 1970). Young plants of *Metrosideros* are normally established along flow margins within four years after the new lava surface is laid down (Smathers & Mueller-Dombois, 1974). After 20 years, the entire flow area is usually stocked with young *Metrosideros*, provided there is a seed source within 1 km. As the stand ages, lichens (*Stereocaulon vulcani*) and ferns (*Nephrolepis exaltata* and others) form a gradually closing surface mat, invaded by clubmoss (*Lycopodium cernuum*), a sedge (*Machaerina angustifolia*), and the mat-forming stoloniferous fern *Dicranopteris linearis*. With greater stand age (over 150 years) *Metrosideros* attains greater stature and crown cover, and tree ferns (*Cibotium glaucum*) enter the stand while *Dicranopteris* declines with increasing shade. This idealized pattern assumes that alien plant species do not disrupt the succession. So far, alien plant invasion has not occurred on a broad scale, although the alien grass *Andropogon virginicus* has entered intermediate stages of the successional sequence in moist areas, usually in conjunction with fire.

In the absence of new volcanic activity, leaching of soils leads to development of soil toxicity. Soil acidity increases with time to pH values of less than 4. Such low pH values promote Al, Fe, and Mn toxicity. Nevertheless, soils at least three million years old on the island of Kauai still support closed stands of *Metrosideros*-dominated rainforests (Mueller-Dombois, 1987a).

In the 1970s, much concern arose because of major stand-level dieback of *Metrosideros* on Hawaii. Death of virtually all canopy trees in entire stands had moved through and affected about half of an 80,000-ha-area of rainforest on the eastern slopes of Mauna Loa and Mauna Kea from the 1950s through 1970s (Burgan & Nelson, 1972; Petteys et al., 1975; Hodges et al., 1986). The phenomenon was initially thought to be caused by a pathogen. A decade of disease research showed that the only two biotic agents considered important (the root fungus *Phytophthora cinnamomi* and the endemic ʻōhiʻa borer *Plagithmysus bilineatus*) were often associated with but not responsible for the dieback (Papp et al., 1979). It was concluded that the trees were dying from another cause (Mueller-Dombois, 1985; Hodges et al., 1986).

Another suggested cause of dieback was flooding of *Metrosideros* root systems after periods of above normal rainfall (Mueller-Dombois & Krajina, 1968). However, analyses of long-term annual

rainfall fluctuations gave no support to this possibility (Doty, 1982; Evenson, 1983). Moreover, stand-level dieback occurred on well-drained and poorly drained sites. Other possible environmental causes, such as drought, sulfur dioxide fumes, and damage by feral ungulates, failed to show any relationship with dieback patterns.

Mueller-Dombois (1983) concluded that many of the dieback stands of *Metrosideros* are in a senescing life stage and that less noticeable climatic perturbations had triggered dieback over the large area. Another possibility is that this dominant species of island forests faces reduced competition and thus invades sites over an extremely broad ecological spectrum, on some of which it is not well adapted (e.g., soils with high aluminum levels or waterlogged soils). As a consequence, it dies periodically over part of its range in response to environmental triggers (Mueller-Dombois, 1986). But no native species is capable of replacing it as a dominant, so *Metrosideros* seedlings reinvade. Jacobi et al. (1983) have determined through analysis of permanent plots that forest dieback is indeed followed in many instances by vigorous regeneration of *Metrosideros*. The predisposing cause for stand-level dieback appears to be the cohort nature of most *Metrosideros* forest stands. After canopy closure of the first-generation forest, *Metrosideros* regeneration is confined to small seedlings only, which remain small and turn over under the canopy without graduating into the sapling life stage. *Metrosideros* seedlings and saplings are recruited into the canopy only after the canopy collapses.

Such synchronous stand dieback is to be expected only in forests with a canopy composed of a single species and thus only (at least in the tropics or subtropics) on islands and mountains where biogeographic isolation has strongly limited colonization by other canopy species (Mueller-Dombois, 1987b). An unfortunate consequence for conservation is that aggressive alien plants can establish on a large scale during a *Metrosideros* dieback event if seed sources are present in the area.

Conclusions

Many island species have an increased degree of vulnerability to extinction (as compared with most continental species) due to their relatively small population size and their adaptation to environments that were free of human disturbance, grazing pressure, and frequent fires until very recently. Although their evolutionary history in isolation has included harsh natural disturbances associated with volcanism and climatic instabilities, their evolution has favored different survival strategies from those used so successfully by the weedy alien invaders. Other island species cope more adequately with alien invaders. Most alien plants notably lack competitive superiority over natives in extreme habitats, such as on new lava flows, on soils with aluminum toxicity, and in montane bogs. Island ecosystems, especially in Hawaii, have been damaged irreparably in the past through underestimating the potential resilience of endemic biota and thus rationalizing their destruction. A more desirable approach for conservation lands involves active management, largely through feral animal control, that will allow survival of most native species as well as watershed protection.

Approximately 177 native Hawaiian vascular plants (over 10% of the total flora) are extinct or thought to be so; roughly half of the surviving native taxa are considered threatened or endangered (Wagner et al., 1985). Many of the extinctions were the direct result of habitat destruction by humans. Further extinctions are expected in communities that survive marginally with already much-reduced species diversity on conservation lands, where the primary threats are feral animals and the alien plant invasions that accompany feral animal activity. Although the situation in the Hawaiian Islands is desperate, recognition of the problem seems to be increasing within and outside the state of Hawaii, and we are guardedly optimistic that the necessary steps will be taken to protect critical ecosystems while they are still ecologically viable.

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SPECIES OF AMARANTHACEAE IN THE GALAPAGOS ISLANDS AND THEIR AFFINITIES TO SPECIES ON THE SOUTH AMERICAN MAINLAND

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Abstract

Roughly 70% of the taxa (including subspecies) of Amaranthaceae in the Galápagos Islands are endemic. About 29 species in seven genera are known from the islands. The subspecies of *Alternanthera filifolia* are the results of an adaptive radiation similar to that of the Darwin Finches and several other groups of island organisms. Some species closely allied to *A. filifolia* represent branches of the same evolutionary tree and could perhaps be accommodated as subspecies within that species. Most of the endemic species of Amaranthaceae are allied to species on the mainland of western South America. The closest affinities of some species of *Alternanthera* seem to be with species in Chile and Peru rather than Ecuador. Floral details and pollen morphology indicate a relationship of the two endemic *Lithophila* species with *Blutaparon*. *Alternanthera albotomentosa* and *A. pubiflora* are reported as new to the islands.

The Amaranthaceae are well represented in the Galápagos Islands, with about 29 species in seven genera. Infraspecific taxa have been recognized in two genera, which gives a total of 38 amaranthaceous taxa found on the islands. Twenty-seven (71%) of these taxa are probably endemic, although one species of *Amaranthus* is almost identical in floral structure with a North American species and two or three taxa of *Alternanthera* are morphologically close to plants from Chile and southern Peru. Several of the endemics are conspicuous elements in the Galápagos flora. The family as a whole includes many widespread weeds. Several of these are now present in the Galápagos. Four species are likely to have reached the islands during the last decades, namely *Achyranthes aspera* L., *Alternanthera caracasana* HBK, *A. mexicana* (Schlechter) Hieron. (= *A. lehmannii* Hieron.), and *A. sessilis* (L.) DC. Additional species likely to become introduced into the archipelago in the future are *Alternanthera pungens* HBK, *Cyathula achyranthoides* (HBK) Moquin, and *Gomphrena celosioides* Martius. The total numbers of species and genera given by way of introduction do not include *Iresine*. The sole record of this genus is based on an evidently mislabeled specimen from the Ecuadorean coast (Eliasson, 1985).

Genera of Amaranthaceae

The genera of Amaranthaceae known from the Galápagos are (number of species in parentheses after each genus) *Pleuropetalum* (1), *Amaranthus* (8), *Achyranthes* (1), *Froelichia* (2), *Alternanthera* (14), *Lithophila* (2), and *Blutaparon* (1). The single species of *Pleuropetalum* is the type species of the genus and is endemic to the islands. It is a 1–2-m-tall shrub known from the islands of Isabela, Santiago, and Santa Cruz.

AMARANTHUS

Amaranthus is the best-known genus in the family, mainly because several species are common weeds in tropical and temperate regions. The genus comprises some 50 or 60 species. In the

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Galápagos, eight species are known, three of which are endemic: *A. anderssonii* Howell, *A. furcatus* Howell, and *A. sclerantoides* (Anderss.) Anderss. The first species is a very weak endemic that is almost identical in floral morphology with *A. berlandieri* (Moq.) Uline & Bray, a species of Texas and northeastern Mexico (Eliasson, 1985). A fourth species, *A. squamulatus* (Anderss.) Robins., was long considered to be endemic but is now known also from the Ecuadorean mainland. *Amaranthus furcatus* and *A. sclerantoides* deviate from the majority of species in the genus in their small size, linear or narrowly obcordate leaves, and certain floral characteristics. Their affinities with mainland species are doubtful, although there are some similarities in floral structure with species such as *A. peruvianus* (Schauer) Standley, a highland plant of Peru, Bolivia, and Argentina, and *A. acutilobus* Uline & Bray, a mainly Mexican species. The narrow leaves in the two Galápagos species are probably an adaptation to the arid conditions.

ALTERNANTHERA

Alternanthera is one of the three largest genera of the Amaranthaceae, the other two being *Gomphrena* and *Ptilotus*. *Alternanthera* is mainly a genus of the New World, but a few species are native to the Old World. The genus has been estimated to contain some 170–200 species, but the true number is probably considerably lower. Some widely distributed weeds are variable and may comprise several morphologically recognizable forms. I have refrained from doing recent research on the genus in the Galápagos, as Dr. James Mears has been working on the group for several years. Some general comments will be given, however.

In the Wiggins & Porter, *Flora of the Galápagos Islands* (1971), I recognized ten species of *Alternanthera*, six of which were regarded as endemic. In one of the endemics, *A. filifolia* (Hooker f.) Howell, seven subspecies were accepted. Even within the subsp. *filifolia* it is possible to recognize several morphologically distinct populations, the differences among which are often vague, however, and intermediate populations or individuals may be found. Whether or not *A. flavicoma* (Anderss.) Howell and a few other taxa should be accommodated as subspecies within *A. filifolia* is largely a matter of personal judgment. They are likely, however, to be branches of the same evolutionary tree as are the entities of *A. filifolia*. The latter species and its subspecific taxa are the results of an adaptive radiation similar to that of the Darwin Finches.

Within the wide range of morphological variation exhibited by *Alternanthera* in the Galápagos, *A. rugulosa* (Robins.) Howell is at the one extreme, *A. nesiotes* Johnston at the other. *Alternanthera rugulosa* forms a small tree 3–4 m tall. It is a rarely collected species known only from San Cristóbal. *Alternanthera nesiotes* is a prostrate plant with a solid vertical taproot and suborbicular leaves 4–8 mm wide. It grows on lava gravel at low elevations on the island of Floreana, where it appears to have a very restricted distribution. The leaves are often about the same color as the lava, which makes the plant easily overlooked.

The most curious distribution pattern of all species of *Alternanthera* in the Galápagos is found in *A. galapagensis* (Stewart) Howell (Fig. 1). It is known from the islets off the coast of Floreana but not from the main island of Floreana. During fieldwork in the archipelago in 1966–1967, I collected a single specimen at Academy Bay. As far as I can see, however, this plant was the result of a casual dispersal; the islets off the coast of Floreana seem to be the only distribution area of the species.

Alternanthera echinocephala (Hooker f.) Christoph. is allied to mainland species but appears to be sufficiently different to be maintained as a species endemic to the Galápagos. A plant described from Hawaii as *A. menziesii* St. John is the same species and was certainly collected in the Galápagos by Archibald Menzies during his short stop on Isabela in February 1795 during the so-called Vancouver Expedition to Hawaii (Mears, 1977), thus a case similar to that of *Scalesia menziesii* (Degener & Sherff) Degener & Sherff.

FIGURE 1. *Alternanthera galapagensis* is a low-growing endemic species with semisucculent glaucous leaves. It has a strange distribution in so far as it is restricted to the islets off the coast of Floreana. There is a possibility that the species was once present on the main island of Floreana but has been eradicated there by introduced browsing animals; if so, this is a good example of the great importance that even very small islets may have for conservation and the survival of species. Photo: U. Eliasson, 5 Dec. 1966, Gardner-near-Floreana.

LITHOPHILA

Lithophila has two endemic species in the Galápagos Islands. The third species in the genus, *L. muscoides* Swartz, is restricted to the West Indies. All three species were originally described as species of *Alternanthera* but they differ fundamentally in androecial and gynoecial morphology. In the Galápagos *L. radicata* (Hooker f.) Standley is a coastal plant growing on lava gravel on the three southeastern islands in the archipelago, Floreana, Española, and San Cristóbal. It is also known from Pinzón. There is some variation among different populations, but the differences observed are not statistically significant. *Lithophila subscaposa* (Hooker f.) Standley is a highland species inhabiting rocky places on Santiago and Floreana. It is also known from a single collection (A. Stewart) from Pinzón. Specimens from Santiago differ in some respects from specimens from Floreana (Eliasson, 1985).

Lithophila subscaposa has lanceolate and obtuse leaves, whereas those of *L. radicata* are subulate and pointed. This difference is obviously a result of adaptations to the different habitats. Agreement in floral details points to a close relationship between these two Galápagos species. On the other hand, their affinity to the Caribbean *L. muscoides* is not necessarily so close as its present assignment to the same genus would suggest. There are some differences in the structure of the androecia. The Galápagos species have a staminodial tooth in the place of each of the three missing stamens, whereas staminodial teeth are not distinct in the Caribbean species (Eliasson, 1985, 1988). There are also differences, albeit slight, in the ornamentation of the pollen grains. Although the pollen of all three species is basically similar and represents the so-called Gomphrena type, that of *L.*

muscoides has almost smooth ridges forming a net on its surface, whereas the ridges in the two Galápagos species are undulate (Eliasson, 1988).

In floral details *Lithophila* is much closer to *Blutaparon* than to *Alternanthera*. The structure of the gynoecium is basically the same in the first-mentioned two genera but different in *Alternanthera*. Further, if three of the five anthers in a flower of *Blutaparon* were reduced, an androecium similar to that of a *Lithophila* would result. The genera have pollen of the same type. Pollen ornamentation in the single Galápagos species of *Blutaparon* is quite similar to that of the two Galápagos species of *Lithophila* (Eliasson, 1988).

BLUTAPARON

The endemic species *Blutaparon rigidum* (Robins. & Greenm.) Mears is the strangest and most fascinating of all the Amaranthaceae in the Galápagos. It was first collected by Georg Baur in August 1891 at Orchilla Bay on Santiago. It has only been collected once since, namely by Alban Stewart in 1905 or 1906. It was originally described as an *Alternanthera* (Robinson & Greenman, 1895) and later, due to its floral morphology, transferred to *Philoxerus* (Howell, 1933). Mears (1982) divided *Philoxerus* into two genera, and referred the Galápagos plant and another three species to the new genus *Blutaparon;* the name *Philoxerus* was retained for Australasian species. In vegetative morphology, *B. rigidum* is very deviant from all other species in the genera mentioned. It is a low shrubby plant with subulate, hard, pungent leaves 3–4 mm long. The sclerophylly and sclerocauly are adaptations to the arid conditions in the Galápagos Islands.

As already mentioned, *B. rigidum* has only been collected twice. Nobody seems to know the exact location of "Orchilla Bay," the type locality on Santiago. It is probable that Stewart's collection, which was annotated to have been taken on the northeastern side of the island, originated from the same locality as Baur's type collection. Later expeditions have searched in vain for the species. Although I have suggested (Eliasson, 1985) that, at least if goat-bitten and sterile, it might be mistaken for *Borreria ericifolia* Hooker f., it may be extinct. This is an assumption held by many botanists with field experience from Santiago. For good reasons, goats have been blamed for its supposed disappearance. As Mears (1982) pointed out, however, an alternative and highly plausible cause of extinction might have been the volcanic activity that occurred in the northeastern part of Santiago between 1897 and 1907, covering a vast area in this part of the island with lava.

Features of floral morphology and pollen structure hint to an evolutionary relationship at least between the Galápagos species of *Lithophila* and *Blutaparon*. Further evidence on evolutionary connections could perhaps be sought in the structure and number of chromosomes. However, without access to live material of *B. rigidum*, it may not be possible to solve the problem regarding the affinity of this strange species. Although the odds are bad, future expeditions to Santiago should watch for *Blutaparon*.

Distributional Categories

Species of Amaranthaceae in the Galápagos Islands fall within one of three distributional categories: (1) endemic species, (2) species restricted to western South America and the Galápagos, and (3) widespread tropical weeds. Rather few species fall within the second category, for example, *Alternanthera albotomentosa* Suesseng. (mainland distribution Ecuador and Peru), *A. pubiflora* (Bentham) Kuntze (Central America to Chile), and *Amaranthus squamulatus* (Ecuador).

Most of the Galápagos endemics have their closest relatives on the mainland of western South America. Examples are (supposedly closest relatives within parentheses) *Pleuropetalum darwinii* Hooker f. (*P. pleiogynum* (Kuntze) Standley) and *Alternanthera echinocephala* (*A. albosquarrosa* Suesseng., *A. pubiflora*). The two endemic species (five taxa) of *Froelichia* are probably derived

from the widespread (Texas to Chile) *F. interrupta* (L.) Moquin. The closest affinities of several species of *Alternanthera* seem to be with species in Chile and Peru rather than Ecuador (Eliasson, 1971). This holds for *A. filifolia*, *A. rugulosa*, and *A. vestita*. Further investigations are needed of species in Chile and Peru before the relationships are fully understood. The affinities of *A. nesiotes* and *A. galapagensis* are still obscure.

Floristic Comments

Two species mentioned in this paper as occurring in the Galápagos have not been reported formally from the archipelago previously and may warrant some further comments. For full descriptions and discussions of taxonomic relationships of the two species, the reader is referred to Eliasson (1987).

Alternanthera albotomentosa Suesseng. *Representative specimens:* Santa Cruz, the central highland and the south slope of the island, 70–850 m, Sep.–Nov. 1966, *Eliasson 155, 268, 282, 392, 397, 445, 542, 583* (all in S). This is the broad-leaved *Alternanthera* (in Galápagos literature often referred to as "*A. halimifolia*") common in the highlands of Santa Cruz. The Galápagos material is intermediate in amount of vestiture between specimens from Ecuador and Peru.

Alternanthera pubiflora (Bentham) Kuntze. *Specimens studied:* Gardner-near-Española, 2–40 m, Dec. 1966, *Eliasson 707–709* (S). A low shrubby plant somewhat reminiscent of *A. echinocephala*. Birds are likely to have carried this species from the mainland.

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REPRODUCTIVE BIOLOGY OF GALAPAGOS ISLANDS ANGIOSPERMS[1]

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ABSTRACT

In recent years there has been an increased interest in the role breeding systems play in the establishment of oceanic island floras. Studies that relate to the Galápagos Islands are discussed. The results of these studies yield a total of 50 species classified as self-compatible and one species classified as self-incompatible. It is suggested that on the Galápagos Islands there has not been a selective drive toward evolution of dioecism and that dioecious plants are not favored in establishment. Instead, hermaphroditic and dioecious plants occur in approximately the same proportions as found in their mainland source areas. Of the two hermaphroditic breeding strategies discussed, self-compatibility and self-incompatibility, the former is highly represented in the Galápagos flora.

BREEDING SYSTEMS IN ISLAND PLANTS

Many obstacles to plant survival are posed by immigration to oceanic islands. Problems that must be overcome by an angiosperm when colonizing such islands include seed transport, germination, and establishment. If a propagule is successfully dispersed it still faces the ecological problem of reproducing in order for the individual to contribute genes to succeeding generations. Many disseminules may reach an island, but only those that land in favorable habitats have a chance of becoming established, growing to maturity, and reproducing.

The question of which breeding system is favored in the establishment of oceanic island floras has been the basis for much discussion (Baker, 1953a, b, 1955, 1966, 1967; Carlquist, 1966; Gilmartin, 1968; De Nettancourt, 1977; Ehrendorfer, 1979; Lloyd, 1980, 1982; Thomson & Barrett, 1981; Bawa, 1982; Willson, 1982; Anderson & Stebbins, 1984; Baker & Cox, 1984). Baker (1955) suggested that self-compatible individuals are favored since a single propagule is sufficient to start a sexually reproducing colony. His studies on the Plumbaginaceae indicated how the breakdown of a self-incompatibility system might be utilized in long-distance dispersal and colonization of islands (Baker, 1953a, b, 1966). Ehrendorfer (1979) stated that "there is good evidence from a number of plant genera that island biota have been successfully colonized by autogamous representatives from among normally outbreeding continental populations."

Carlquist (1966), by contrast, proposed that dioecy, which results in variability because of obligatory outcrossing, is so important that the necessary establishment of two propagules is not an overpowering disadvantage for colonizing an island. He estimated that dioecious species constitute 27.7% of the Hawaiian flora, 14.5% of the New Zealand flora, and only 2.6% of the California flora. These values seemed to substantiate his hypothesis on dioecious immigrant stock.

Baker (1967) pointed out that the high incidence of dioecism found on some islands could in fact

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support his views on establishment. He proposed that if, as Carlquist (1966) stated, the need for arrival of two dioecious plants at the same time is not a severe impediment to colonization, then the establishment of two hermaphroditic self-incompatible plants of a certain species would be even more likely. This is because in a homomorphic self-incompatibility system the chances are good that the two plants will be cross-compatible, while for dioecious species the chances are only 50% that an appropriate mate will be present. This suggests that there should be a high proportion of self-incompatible plants on oceanic islands relative to dioecious plants. This was not found to be the case for Hawaii, New Zealand, and the Galápagos (Carlquist, 1966, 1974; Rick, 1966; Pandey, 1979; Lloyd, 1980; Thomson & Barrett, 1981). Baker (1967) attributed this to the fact that dioecy appears to be more easily evolved than self-incompatibility. Baker & Cox (1984) suggested that "the mere alteration of the hormone system in a plant can produce separate staminate or pistillate flowers even on the same shoot (as in monoecious plants) without genetical difference." Baker (1959) had stated earlier that dioecy can also be reached quite simply through a few genetic changes. The evolution of a self-incompatibility system requires the more demanding formation of a multiple allele system. Baker (1967) suggested that dioecy could evolve from hermaphroditic or monoecious immigrants that lacked self-incompatibility mechanisms, and that were pushed by selection pressures toward outcrossing devices. Thomson & Barrett (1981) claimed along the same line that "self-compatible hermaphrodites have more often established small populations on true islands or 'habitat islands' and selection for outcrossing then favors the evolution of dioecy."

Tempering hypotheses of evolution of dioecy after colonization, Bawa (1982) disagreed with Thomson & Barrett's (1981) claim that the autochthonous development of dioecism on islands is frequent. He pointed out that, of 38 nonendemic genera with sexually dimorphic species in Hawaii, only four appear to have representatives where sexual dimorphism is confined to the island chain. Moreover, in New Zealand, out of 66 nonendemic genera with sexually dimorphic species, only five are confined to the islands. Bawa noted that, along with the gains in fitness resulting from outcrossing that might favor dioecious species, three additional factors help explain the high rate of dioecism observed on some islands: (1) The fruits and seeds of dioecious taxa may be more successful than those of hermaphroditic species in reaching an island because many dioecious species have fleshy fruits and seeds that are often dispersed by animals, and Carlquist (1974) emphasized the importance of birds in colonization of islands. (2) He suggested that the high incidence of dioecy on some islands may be because islands are usually inhabited by small generalist insects, and there is a strong correlation between dioecy and pollination by such insects. (3) There is a high proportion of perennial woody species in island floras, and dioecy is more common in trees and shrubs than in herbaceous species.

Baker & Cox (1984) added that establishment of dioecious plants might also be facilitated by "leakage" in the breeding system. In other words, a dioecious plant may occasionally form flowers of the opposite sex or perfect flowers, which would allow for seed set.

Anderson & Stebbins (1984) suggested that dioecy might be more efficient in outcrossing when the population in question is small or composed of closely related individuals, because in these situations there may be too few S-alleles for the correct functioning of a gametophytic self-incompatibility system.

The Galapagos Flora

The Galápagos Islands are appropriate for a study of plant breeding systems on oceanic islands since they lie some 800 km west of the coast of Ecuador and have been isolated long enough for a distinct flora to evolve. In addition, all indigenous members have probably reached the islands via long-distance dispersal.

The angiosperm flora of the Galápagos Islands is composed of 494 indigenous species, subspecies, and varieties, 216 of which are endemics. Also present are 259 exotics, which brings the total number of flowering plant taxa in the archipelago to 753 (Lawesson et al., 1987).

FIGURE 1. Female carpenter bee (*Xylocopa darwini*) visiting an inflorescence of *Prosopis juliflora*. Pollen is visible on the bee's thorax.

Seven endemic genera of angiosperms inhabit the islands: *Darwiniothamnus*, *Lecocarpus*, *Macraea*, and *Scalesia* of the Asteraceae; *Brachycereus* and *Jasminocereus* of the Cactaceae; and *Sicyocaulis* of the Cucurbitaceae. There are several monoecious endemics, but only *Baccharis steetzii* (Asteraceae), *Bursera malacophylla* (Burseraceae), *Croton scouleri* (Euphorbiaceae), and *Castela galapageia* (Simaroubaceae) are dioecious endemics. These plants belong to genera that are dioecious elsewhere, making it unlikely that they evolved dioecy after entry to the Galápagos. Lloyd (1980) mentioned that the high percentage of self-fertilization thought to exist on the Galápagos Islands might be due to their relatively young age, as well as to their poor insect fauna and open habitat. Baker & Cox (1984) attributed the low percentage of dioecy to the inherent dryness of the archipelago, and Carlquist (1974) stated that they may not show the predicted insular tendencies because they are of a more recent origin than the Hawaiian Islands and New Zealand.

The flora of the archipelago may be divided into seven major vegetation zones: Littoral, Arid, Transition, Scalesia, Zanthoxylum, Miconia, and Pampa zones (Wiggins & Porter, 1971; van der Werff, 1978, 1979). These zones are, in turn, included in three major ecological zones (Johnson & Raven, 1973). They are (1) Littoral, (2) Basically Arid (including the Arid and Transition Zones of vegetation), and (3) Basically Mesic (including the Scalesia, Zanthoxylum, Miconia, and Pampa zones of vegetation).

Pollination in Galapagos Plants

There are few insect pollinators within the Galápagos archipelago. In fact, only one species of bee, *Xylocopa darwini* (Fig. 1), is represented on the islands (Cockerell, 1935; Hurd, 1958). Rick (1963, 1966), Linsley et al. (1966), and McMullen (1985) have studied its role as a pollinator on

Santa Cruz. The depauperate condition of the Galápagos insect fauna in general is emphasized by the relative dearth of other representative types (Linsley & Usinger, 1966; Rindge, 1973; Hayes, 1975; Linsley, 1977), and few reports have been made as to what flowering plants are visited by these insects (Williams, 1911; Beebe, 1923; Wheeler, 1924; Hayes, 1975; Grant & Grant, 1981; McMullen, 1986).

Wind is thought to be an important pollination agent on some islands such as Hawaii, New Zealand, and Juan Fernandez (Carlquist, 1965; Ehrendorfer, 1979; Thornton, 1971). Rick (1966) found no evidence of wind pollination in his study of the Galápagos but later stated that anemophilous groups, such as the Poaceae and Euphorbiaceae, are well represented in the flora (Rick, 1983).

Breeding Strategies for Galapagos Plants

Rick (1966) studied the breeding systems of 17 angiosperm species on Santa Cruz during a five-week period. Most of the species studied were located near Academy Bay, in the lowlands of this island. The species included *Castela galapageia* (Simaroubaceae); *Cardiospermum galapageium* (Sapindaceae); *Jasminocereus thouarsii* var. *delicatus* (recorded as *J. howellii*), *Opuntia echios* (var. *gigantea*) (Cactaceae); *Stictocardia campanulata* (recorded as *S. "tiliaefolia"*) (Convolvulaceae); *Cordia leucophlyctis* (recorded as *C. galapagensis*), *Cordia lutea*, *Tournefortia rufosericea* (Boraginaceae); *Acnistus ellipticus*, *Lycium* (*minimum*), *Lycopersicon cheesmanii* var. *cheesmanii* (recorded as *L. pimpinellifolium*) (Solanaceae); *Nolana galapagensis* (recorded as *Peraliloba galapagensis*) (Nolanaceae); *Justicia galapagana* (Acanthaceae); *Borreria* sp., *Chiococca alba* (Rubiaceae); *Scalesia affinis*, and *S. helleri* (Asteraceae). The results for the first four of these species were inconclusive. The remaining 13 were classified as self-compatible, with all but *Cordia lutea* considered automatic self-pollinators. In addition, Rick also found *Scalesia aspera* to be an automatic self-pollinator from studies he performed on this plant in cultivation. He concluded that automatic self-pollinators had been favored in establishment on the islands. The carpenter bee *Xylocopa darwini* was observed at flowers of nine of these species. No pollinators were observed for seven of the species, and one was visited by dipteran species. The cactus finch, *Geospiza scandens*, visited the flowers of *Opuntia echios*, which Rick mentioned as often damaged during the visits.

Grant & Grant (1981) studied the breeding behavior of *Opuntia helleri* on Genovesa and classified it as self-incompatible. Although some selfing occurred, outcrossing increases seed set greatly. They reported plants of *Opuntia* to be visited by finches, mockingbirds, doves, crickets, dipteran flies, and ants, and that these may be potential pollinators. And they suggested that *Opuntia* may depend on birds for pollination on islands where the carpenter bee is absent, as on Genovesa.

McMullen (1987) studied the breeding strategies of 52 angiosperm species from 30 families on Santa Cruz. Since dioecy is present in only 3% of the Galápagos flora (Baker & Cox, 1984), this study was undertaken to determine if self-incompatibility was more prevalent than previously thought, acting as an enforcer of outcrossing, or, if instead, both of these obligatory outcrossing mechanisms were poorly represented and self-compatibility was the rule.

Fieldwork for this study was conducted on the southern slope of Santa Cruz. Quadrats were established and plants tested in each of the seven vegetation zones. Figure 2 shows the locations and altitudes of the quadrats. The results of the bagging experiments are shown in Table 1. Along with the plant name is its resident status, vegetation zone in which the tests were made, and the insects that visited the flowers.

Of the 52 species studied, 51 are hermaphroditic; only *Croton scouleri* var. *scouleri* is dioecious. Of the 51 hermaphroditic species studied, 40 showed some degree of self-compatibility, and 11 yielded inconclusive results. All but three of the self-compatible group—*Cordia lutea* (Boraginaceae), *Diodia radula* (Rubiaceae), and *Gossypium barbadense* var. *darwinii* (Malvaceae)—also

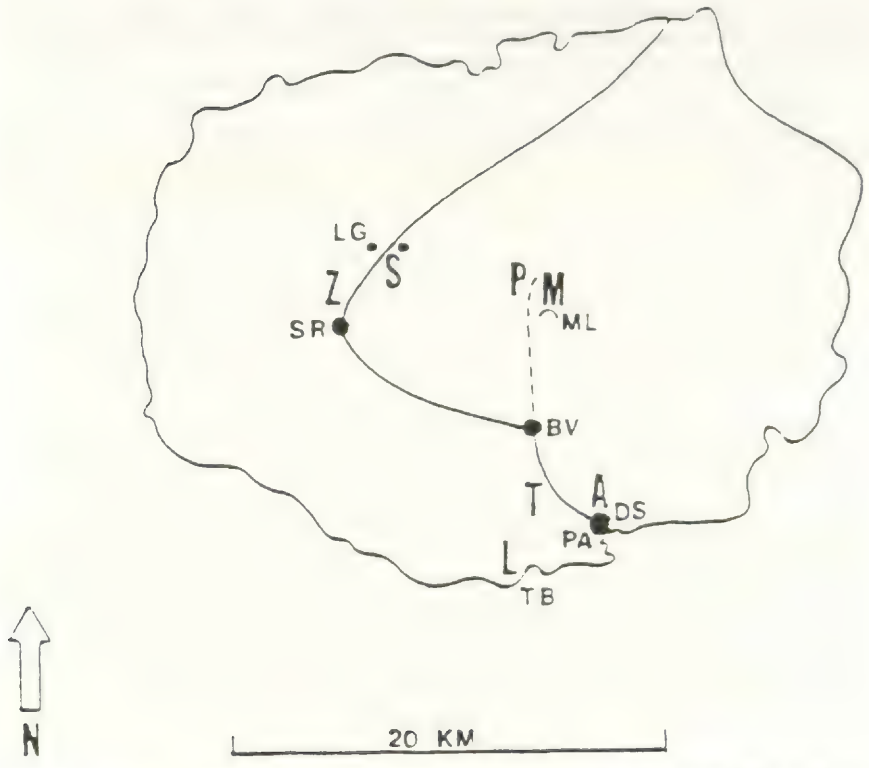

FIGURE 2. Locations and altitudes of study quadrats on Santa Cruz Island (90° 21′ 30″ W, 0° 37′ 33″ S). L = Littoral Zone quadrat, western side of Tortuga Bay (TB) in mangrove area, sea level; A = Arid Zone quadrat, Darwin Station (DS) near dormitories, 10 m; T = Transition Zone quadrat, 3.5 km north of Puerto Ayora (PA) on left side of road to Bella Vista (BV), 50 m; S = Scalesia Zone quadrat, 0.5 km south of the northernmost member of Los Gemelos (LG) near road, 550 m; Z = Zanthoxylum Zone quadrat, north of Santa Rosa (SR) next to farm of Señor Miranda, 420 m; M = Miconia Zone quadrat, north of Media Luna (ML) near small national park building, 500 m; P = Pampa Zone quadrat, 3 km north of Media Luna near trail to El Puntudo.

demonstrated automatic self-pollination. While McMullen (1987) found the results for *Cordia leucophlyctis* and *Acnistus ellipticus* to be inconclusive, Rick (1966) classified these species as automatic self-pollinators.

The Galápagos carpenter bee, which visits a variety of plants for pollen and nectar, was found to be the major pollinator on Santa Cruz, especially for nonendemic members of the flora; however, nine insects were newly reported as visitors to plants on Santa Cruz, and 24 plant species were newly reported as visited by insects on this island (McMullen, 1985, 1986).

Finches may also act as pollen vectors for some of the plants tested. These birds were observed at the flowers of *Opuntia echios* var. *gigantea* (Cactaceae), *Sida rhombifolia* (Malvaceae), *Prosopis juliflora* (Mimosaceae), *Passiflora foetida* var. *galapagensis* (Passifloraceae), and *Tribulus cistoides* (Zygophyllaceae). Although some of the flowers were damaged during the visits, the possibility of successful pollination does exist (McMullen, 1987).

Floral morphologies conducive to wind pollination were rarely encountered during this study. The amount of pollen produced by most of the species tested was quite low. These results, along with similar observations by Colinvaux & Schofield (1976), suggest that anemophily has been selected against.

TABLE 1. Breeding systems and insect visitors of plants studied. Plant data include resident status and vegetation zone where tests were performed. ASP = automatic self-pollination, NASC = nonautomatic self-compatibility, DIO = dioecy, INR = inconclusive results.

Plants studied	Breeding systems	Insect visitors
ACANTHACEAE		
Justicia galapagana	ASP	*Leptotes parrhasioides* (Lycaenidae)
Endemic		*Wasmannia auropunctata* (Formicidae)
Transition Zone		*Xylocopa darwini* (Apidae)
Tetramerium nervosum	ASP	
Native		
Pampa Zone		
AMARANTHACEAE		
Alternanthera echinocephala	ASP	
Native		
Arid Zone		
APOCYNACEAE		
Vallesia glabra var. *glabra*	INR	
Native		
Arid Zone		
ASTERACEAE		
Adenostemma platyphyllum	ASP	
Introduced weed		
Zanthoxylum Zone		
Ageratum conyzoides	ASP	*Toxomerus crockeri* (Syrphidae)
subsp. *conyzoides*		
Introduced weed		
Pampa Zone		
Bidens pilosa	ASP	
Introduced weed		
Zanthoxylum Zone		
Darwiniothamnus tenuifolius	ASP	
subsp. *tenuifolius*		
Endemic		
Scalesia Zone		
Jaegeria gracilis	ASP	*Toxomerus crockeri*
Endemic		
Pampa Zone		
Scalesia pedunculata	ASP	*Xylocopa darwini*
Endemic		
Scalesia Zone		
AVICENNIACEAE		
Avicennia germinans	ASP	*Paratrechina longicornis* (Formicidae)
Native		*Tapinoma melanocephalum* (Formicidae)
Littoral Zone		
BORAGINACEAE		
Cordia leucophlyctis	INR	*Disclisioprocta stellata* (Geometridae)
Endemic		*Xylocopa darwini*
Arid Zone		
C. lutea	NASC	*Metacanthus galapagensis* (Berytidae)
Native		*Paratrechina vaga*
Arid Zone		*Wasmannia auropunctata*
		Xylocopa darwini

TABLE 1. Continued.

Plants studied	Breeding systems	Insect visitors
Tournefortia psilostachya	ASP	*Leptotes parrhasioides*
Native		Unidentified moth (Pyralidae)
Arid Zone		
T. pubescens	ASP	
Endemic		
Arid Zone		
T. rufo-sericea	ASP	
Endemic		
Transition Zone		
CACTACEAE		
Opuntia echios var. *gigantea*	INR	
Endemic		
Arid Zone		
CAESALPINIACEAE		
Parkinsonia aculeata	ASP	*Xylocopa darwini*
Native		
Arid Zone		
Cassia occidentalis	INR	*Xylocopa darwini*
Native		
Transition Zone		
CYPERACEAE		
Cyperus elegans subsp. *rubiginosus*	ASP	
Endemic		
Arid Zone		
EUPHORBIACEAE		
Croton scouleri var. *scouleri*	DIO	
Endemic		
Arid Zone		
FABACEAE		
Vigna luteola	INR	*Leptotes parrhasioides*
Native		*Xylocopa darwini*
Pampa Zone		
LAMIACEAE		
Hyptis rhomboidea	ASP	
Introduced weed		
Pampa Zone		
LOBELIACEAE		
Lobelia xalapensis	ASP	
Native		
Pampa Zone		
LYTHRACEAE		
Cuphea racemosa	ASP	*Leptotes parrhasiodes*
Introduced weed		*Toxomerus crockeri*
Pampa Zone		
MALVACEAE		
Bastardia viscosa	ASP	*Xylocopa darwini*
Native		
Arid Zone		
Gossypium barbadense var. *darwinii*	NASC	*Phoebis sennae* (Pieridae)
Endemic		
Arid Zone		

TABLE 1. Continued.

Plants studied	Breeding systems	Insect visitors
Sida rhombifolia	ASP	*Leptotes parrhasioides*
Introduced weed		*Xylocopa darwini*
Scalesia Zone		
MELASTOMATACEAE		
Miconia robinsoniana	INR	
Endemic		
Miconia Zone		
MIMOSACEAE		
Acacia macracantha	INR	
Native		
Arid Zone		
Prosopis juliflora	ASP	*Tapinoma melanocephalum*
Native		*Xylocopa darwini*
Littoral Zone		
NYCTAGINACEAE		
Commicarpus tuberosus	ASP	*Leptotes parrhasioides*
Native		
Arid Zone		
ORCHIDACEAE		
Epidendrum spicatum	INR	
Endemic		
Zanthoxylum Zone		
Habenaria monorrhiza	ASP	
Native		
Pampa Zone		
Ionopsis utricularioides	INR	
Native		
Zanthoxylum Zone		
PASSIFLORACEAE		
Passiflora colinvauxii	INR	
Endemic		
Scalesia Zone		
P. foetida var. *galapagensis*	ASP	*Xylocopa darwini*
Endemic		
Arid Zone		
PIPERACEAE		
Peperomia galapagensis	ASP	
var. *galapagensis*		
Endemic		
Scalesia Zone		
PLUMBAGINACEAE		
Plumbago scandens	ASP	*Leptotes parrhasioides*
Native		*Phoebis sennae*
Transition Zone		
POACEAE		
Paspalum conjugatum	ASP	
Cultivated escape		
Scalesia Zone		
Setaria geniculata	ASP	*Wasmannia auropunctata*
Native		
Arid Zone		

TABLE 1. Continued.

Plants studied	Breeding systems	Insect visitors
POLYGONACEAE		
Polygonum opelousanum	ASP	*Toxomerus crockeri*
Native		
Pampa Zone		
PORTULACACEAE		
Portulaca oleracea	ASP	
Introduced weed		
Arid Zone		
RHAMNACEAE		
Scutia spicata var. *pauciflora*	ASP	
Endemic		
Arid Zone		
RUBIACEAE		
Diodia radula	NASC	*Toxomerus crockeri*
Introduced weed		
Scalesia Zone		
SOLANACEAE		
Acnistus ellipticus	INR	
Endemic		
Zanthoxylum Zone		
Capsicum frutescens	ASP	*Wasmannia auropunctata*
Cultivated escape		
Transition Zone		
Lycopersicon cheesmanii	ASP	
var. *cheesmanii*		
Endemic		
Arid Zone		
VERBENACEAE		
Clerodendrum molle var. *molle*	ASP	Unidentified ant (Formicidae)
Native		Unidentified hawk-moth (Sphingidae)
Arid Zone		*Xylocopa darwini*
Lantana peduncularis	ASP	
var. *peduncularis*		
Endemic		
Arid Zone		
Verbena litoralis	ASP	
Introduced weed		
Zanthoxylum Zone		
ZYGOPHYLLACEAE		
Tribulus cistoides	ASP	*Leptotes parrhasioides*
Introduced weed		*Xylocopa darwini*
Arid Zone		

DISCUSSION AND CONCLUSIONS

Combining the results of these three breeding studies yields a total of 50 species classified as self-compatible, one species classified as self-incompatible, and 12 species with inconclusive results. If only indigenous plants are considered, the figure for self-compatible species becomes 38 when using Porter's (1983) listing of introduced weeds and cultivated escapes, and 44 if Lawesson et al. (1987) is followed. These indigenous plants are of most interest since they reflect the natural

processes occurring in the Galápagos Islands, and not the breeding systems of recently introduced species.

McMullen (1987) suggested that on the Galápagos Islands there has been neither a selective drive toward evolution of dioecism nor are dioecious plants particularly favored in establishment. Instead, hermaphroditic and dioecious plants occur in relatively the same proportions as found in their mainland source areas. Of the two hermaphroditic breeding strategies considered, self-compatibility and self-incompatibility, the former is highly represented in the Galápagos flora.

Conclusions as to whether the high level of self-compatibility found in the Galápagos is the result of a filter effect or an autochthonous origin await studies on mainland breeding strategies. If mainland studies show the Galápagos species or their most closely related sister-taxa to be self-compatible, then the plants probably had this breeding system when they arrived on the islands. If, instead, the mainland counterparts are self-incompatible, then the plants likely evolved self-compatibility after arrival.

The need for continued experimental studies on the Galápagos Islands in general, and Santa Cruz specifically, is urgent. Human activities, along with introduced plants and animals, are changing the natural vegetation in many areas. Already several zones of vegetation on Santa Cruz Island can no longer be investigated in their original condition (van der Werff, 1979). Included among these are the Zanthoxylum Zone and Miconia Zone, which are being used for pastureland or cultivation in some areas. The Pampa Zone is also being threatened, primarily by introduced plants, especially *Cinchona succirubra* (Rubiaceae), a tree that is now taking over in many places.

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HERBACEOUS AND ERICACEOUS COMMUNITIES IN THE HIGHLANDS OF SANTA CRUZ, THE GALAPAGOS ISLANDS[1]

Syuzo Itow[2]

Abstract

The herbaceous and ericaceous vegetation in the highlands of Santa Cruz was studied to find relations of plant communities to topographical relief. The vegetation was classified into six communities according to a scatter diagram of vegetation samples (relevés) processed by the reciprocal averaging method and according to the dominant species. The communities classified are *Paspalum conjugatum* community, *Pteridium aquilinum*/*Blechnum polypodioides* community, *Lycopodium clavatum* community, *Hypericum uliginosum* community, *Polypodium tridens* community, and *Pernettya howellii* community. Of the communities recognized, the *Paspalum conjugatum* community was found on moist, gentle slopes and flat sites. The *Pernettya howellii* community was established on southeast-facing, steep slopes at higher altitudes exposed directly to the southern trade winds. This habitat becomes wet or moistened by moisture-saturated southern winds on cloudy and foggy days, but dries up in extended dry periods. The *Polypodium tridens* community was found only on nearly exposed lava. The three other communities were intermediate between the *Paspalum* community and the *Pernettya* community in phytosociological and topographical relations.

The treeless vegetation in the highlands of Santa Cruz, the Galápagos Islands, was first reported by Howell (1942, 1957: photos 2a, 3a, and 3b). Bowman (1961) called this treeless highland the Upland Zone, while Wiggins & Porter (1971) described it as the Fern–Sedge Zone.

In this treeless highland, Itow & Weber (1974) studied fens and bogs, and van der Werff (1978) described Habenario-Trisetetum howellii as a new plant association and the community of *Sphagnum erythrocalyx* and *Elaphoglossum glosophyllum*. Hamann (1981) investigated broad-leaved herbaceous vegetation during his extensive vegetation studies and described a *Pteridium aquilinum*–*Jaegeria gracilis* community, a *Sphagnum cuspidatum* community, and a *Jaegeria crassa* community in the Santa Cruz highland.

The present study was carried out in the highlands of Santa Cruz in 1970 from the standpoint of phytosociology, to find out what plant communities have developed and how they are related to altitude, slope aspect, and steepness of slope. A part of the study has been published previously (Itow & Weber, 1974). The present paper describes herbaceous and ericaceous plant communities found in the same highlands.

Study Area and Methods

There are basically four vegetation zones on Santa Cruz in terms of climate, ranging from Dry through Transition and Moist to Highland zones, of which the last is treeless. Since the

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southeastern trade winds, which bring moisture to the islands, prevail during most of the year, the north side of the island is drier, and the zones are deflected upward. The treeless vegetation ranges from 560 m altitude on the southern slope to the summit of Mt. Crocker (860 m), and from 670 m to the highest point on the northern side (Itow, 1971). (For an outline map, see Itow & Weber, 1974, fig. 2.)

The area was originally treeless (Howell, 1942, 1957) and is still so. Parts of the area have occasionally been grazed or burnt (Hamann, 1975; van der Werff, 1978).

In 1970, the weather was unusually dry from February through April, and the summit area was visible every day from the south coast of the island. The rain gauge located at the lower boundary of the treeless highland zone (ca. 620 m) received only 147 mm of precipitation in those three months of 1970, while it received 250–800 mm in the same months between 1968 and 1975 (Charles Darwin Research Station, 1968–1975).

In each of the vegetation stands studied, the altitude, slope direction, and steepness of slope were recorded by readings of a pocket altimeter and a hand compass, respectively. Other conditions recognizable in the stand were also recorded.

Vegetation sampling followed Braun-Blanquet's relevé method, using 1–4-m^2 quadrats and adopting Braun-Blanquet's (1964) dominance classes (+, 1–5) and sociability classes. Voucher specimens were determined at Stanford University by Ira L. Wiggins and the author. One set of specimens is deposited in the California Academy of Sciences Herbarium, the other in the Nagasaki University Herbarium.

In Tables 1–5, the dominance and sociability classes of plants are presented together in the normal format (e.g., '4.3'), where the first digit is dominance class and the second is sociability class. The record "+" means the dominance class + and sociability class 1. Prominent bryophytes and lichens are listed in the tables under names given in the field.

The vegetation was classified roughly into three categories: fens and bogs accompanied by *Sphagnum* species, fern–sedge communities, and ericaceous communities. Vegetation samples (relevés) of herbaceous and ericaceous communities were processed with Hill's (1973) reciprocal averaging method (RA) to analyze phytosociological relations of plant communities. This method is effective in ordination of vegetation samples with little distortion and gives a scatter diagram (Gauch et al., 1977).

In compiling the tables of species composition, all the vegetation samples were grouped into communities according to the results obtained by the RA processing. In each of the community tables, the vegetation samples were arranged in order by the method given in Mueller-Dombois & Ellenberg (1974) to find subgroups in species composition within each of the classified communities (Tables 1–5).

Results

Figure 1 shows the scatter diagram of the vegetation samples (except *Polypodium tridens*-dominated stands on account of their extreme positions). Based on their positions on the scatter diagram and based on the dominant species, the 97 vegetation samples, including those dominated by *Polypodium tridens*, were classified into six different communities. They are *Paspalum conjugatum* community (Table 1), *Pteridium aquilinum/Blechnum polypodioides* community (Table 2), *Lycopodium clavatum* community (Table 3), *Hypericum uliginosum* community (Table 4), *Polypodium tridens* community (Table 4), and *Pernettya howellii* community (Table 5). Based on my field experiences in the highlands, the x-axis of the scatter diagram (Fig. 1) can be interpreted as representing a wet-to-dry gradient, but the y-axis is difficult to interpret. Figure 2 gives the distributions of the recognized communities in relation to altitude, slope directions, and slope steepness in degrees.

TABLE 1. *Paspalum conjugatum* community.

Stand number	1	2	3	4	5	6	7	8	9	10	11	12	13
Altitude (m)	650	720	650	690	690	710	690	720	790	680	630	680	680
Slope aspect	NW	SW	—	—	—	—	—	—	NNW	—	—	—	—
Slope (degrees)	25	30	—	—	—	—	—	—	10	—	—	—	—
Numbers of species	15	14	16	12	10	12	10	12	12	6	6	5	3
CHARACTERISTIC SPECIES													
Paspalum conjugatum	5.4	5.4	5.4	1.2	2.2	5.4	5.5	5.4	5.4	5.5	4.4	5.5	5.5
DIFFERENTIAL SPECIES													
Vigna luteola	2.2	.	+.2	+	1.2	+	1.2	2.2	1.2	2.2	.	.	.
Commelina diffusa	.	+	+	+	+.2	2.3	+	+	1.1	2.2	.	.	.
Borreria laevis	3.3	2.2	+.2	3.4	3.3	+	.	+	.	.	.	.	.
Tournefortia rufo-sericea	1.2	2.2	+.2	.	.	.	.	.	.	.	.	.	.
Acnistus ellipticus	(+)	(+)	1.2	.	.	.	.	.	.	.	.	.	.
Panicum glutinosum	2.2	2.2	+.2	.	.	.	.	.	.	.	.	.	.
Justicia galapagana	+.2	(+)	.	.	.	.	.	.	.	.	.	.	.
Psychotria rufipes	.	(+)	1.2	.	.	.	.	.	.	.	.	.	.
Ctenitis pleiosoros	.	+	(+)	.	.	.	.	.	.	.	.	.	.
Hypolepis hostilis	.	+	+	.	.	.	.	.	.	.	.	.	.
COMPANIONS													
Pteridium aquilinum	1.2	2.2	1.2	+	1.2	.	.	3.3	+.2	1.2	2.2	1.1	.
Nephrolepis cordifolia	+.2	.	.	.	.	1.2	1.2	+	+.2	.	.	2.2	2.2
Polygonum opelousanum	.	.	+	5.4	4.4	1.2	.	.	+	1.2	+	.	.
Thelypteris pilosula	+.2	.	.	.	.	+.2	.	.	+.2	+.2	.	+.2	.
Drymaria cordata	.	.	.	+.2	1.2	.	.	+	+	.	.	.	.
Centella asiatica	.	.	.	2.3	3.3	4.4	2.3	.	.	.	.	.	.
Cyperus sp.	.	.	.	+.2	+	+	+	.	.	.	.	.	.
Blechnum occidentale	1.2	(+)	.	.	.	+	.	.	.	.	.	.	.
Alternanthera halimifolia	(+)	.	+.2	.	.	.	.	1.2	.	.	.	.	.
Hyptis rhomboidea	+.2	.	.	.	.	.	.	+.2	.	.	.	.	.
Scleria pterota	.	2.2	.	+.2	.	.	.	.	.	.	.	.	.
Hibiscus diversifolius	.	2.2	.	.	.	.	.	.	.	.	3.3	.	.
Jaegeria gracilis	.	.	1.2	.	.	.	.	+.2	.	.	.	.	.
Scleria hirtella	.	.	.	.	+.2	.	.	.	.	.	2.3	.	.
Panicum dichotomiflorum	.	.	.	.	.	1.2	1.2	.	.	.	.	.	.
Rhynchospora rugosa	.	.	.	.	.	.	2.2	.	.	.	2.3	.	.

Other companions. In stand number 1: *Pilea baurii* +.2, Pteridophyte sp. +; in number 3: *Cissampelos pareira* 1.1, *Zanthoxylum fagara* +.2; in number 4: *Polygonum hydropiperoides* +.2, *Thelypteris* sp. +.2; in number 6: *Oxalis* sp. +; in number 7: *Stenotaphrum secundatum* 1.2, *Eleocharis* sp. +.2; in number 8: *Cyperus grandifolius* +.2, *Phyllanthus caroliniensis* +.2, *Ichnanthus nemorosus* +.2; in number 9: *Drymaria monticola* +.2, *Paspalum galapageium* +.2, *Dichondra repens* (+); in number 12: *Eleocharis* sp. +; in number 13: *Ludwigia leptocarpa* 2.3.

PASPALUM CONJUGATUM COMMUNITY

The *Paspalum conjugatum* community (Table 1) was found on gentle slopes and flat sites mostly at lower elevations in the treeless highland (Fig. 2A). In 1970, the habitat was scarcely dried, not even in long-lasting dry periods without rainfall and fogdrip. The vegetation was approximately one meter high. *Pteridium aquilinum* often co-dominated in rather less moist habitat. Major companions in the *Paspalum conjugatum* community are *Nephrolepis cordifolia*, *Polygonum opelousanum*, *Thelypteris pilosula*, and *Centella asiatica* (Table 1).

The community can be divided into two types. The one was distinguished by the presence of *Vigna luteola* and *Commelina diffusa* (Stands 1–10 in Table 1), and the other by their absence

TABLE 2. *Pteridium aquilinum/Blechnum polypodioides* community.

Stand number	1	2	3	4	5	6	7	8	9	10	11	12	13
Altitude (m)	750	725	690	685	685	700	730	680	560	800	730	640	755
Slope aspect	SE	ESE	NW	SSE	ESE	S	SSE	SE	NNE	SE	NW	SSE	—
Slope (degrees)	20	15	30	25	20	30	10	30	2	30	5	10	5
Numbers of species	10	11	11	9	10	15	11	12	7	7	9	10	8
DOMINANT SPECIES													
Pteridium aquilinum	4.4	4.3	5.4	1.1	2.2	2.2	+.2	1.2	3.3	1.2	4.4	3.2	3.3
Blechnum polypodioides	3.2	5.4	3.3	5.4	5.4	3.4	5.5	5.5	2.2	5.5	2.3	4.4	2.3
DIFFERENTIAL SPECIES													
Vigna luteola	2.2	2.2	.	1.1	+	1.2	.	+	.	.	3.3	1.2	4.4
Conyza bonariensis	.	1.1	+	+	+	+	+	.	.	.	.	.	.
Pityrogramma calomelanos	.	(+)	.	.	.	1.2	1.2	.	(+)	+.2	.	3.4	.
Jaegeria gracilis	.	.	+.2	.	.	.	2.2	.	1.2	+	1.2	.	3.4
Thelypteris pilosula	.	+.2	.	+.2	+	.	.	+	.	+	+.2	+.2	.
Borreria laevis	+	+	.	.	.	.	.	.	.	.	+.2	.	.
COMPANIONS													
Phyllanthus caroliniensis	2.2	1.2	+	1.1	+	2.2	.	2.2	.	+	+	+	+
Hypericum uliginosum	.	.	+	+	1.1	+.2	3.3	1.2	+.2	+.2	.	.	.
Panicum dichotomiflorum	.	.	.	.	.	2.2	.	+.2	.	.	.	.	.
Commelina diffusa	1.2	+.2	.	.	.	.	.	+	.	.	.	.	.
Gramineae sp.	.	.	.	+.2	1.2	.	.	.	.	.	.	.	.
Pilea baurii	.	.	+	.	.	.	.	.	.	.	.	.	.
Cyperus grandifolius	3.3	1.2	.	.	1.2	1.2	.	.	.	.	.	.	.
Hyptis rhomboidea	+	.	.	.	.	+.2	+.2	.	.	.	.	.	+
Centella asiatica	.	(+)	.	.	.	4.4	.	2.3	.	.	.	.	.
Nephrolepis cordifolia	.	.	.	.	.	.	.	1.2	.	.	.	+	.
Paspalum conjugatum	.	.	.	.	.	.	.	.	3.2	.	1.2	.	1.2
Mecardonia dianthera	.	.	+.2	+.2	.	.	+.2	.	.	.	.	.	.
Blechnum occidentale	.	.	+	.	.	.	.	.	.	.	.	.	.
Polygonum opelousanum	+.2	.	.	.	.	+	.	.	.	.	.	.	1.2
Drymaria monticola	+	.	.	.	.	+.2	.	.	.	.	.	.	.
Ophioglossum reticulatum	.	.	.	.	+	.	.	.	+	.	.	.	.
Drymaria cordata	.	.	.	.	.	.	+.2	.	.	.	.	.	.
Thelypteris sp.	.	.	.	.	.	.	+.2	+.2	.	.	.	.	.
(Brown hepatics)	.	.	.	.	.	.	.	.	.	.	.	.	.
Justicia galapagana	.	.	.	.	.	+	.	.	.	.	.	.	.
Paspalum sp.	.	.	.	.	.	.	.	+.2	.	.	.	.	.
Cladonia spp.	.	.	.	.	.	.	.	.	.	.	.	.	.

Other companions. In stand number 3: *Paspalum galapageium* var. *minoratum* +.2, Pteridophyte sp. +; in number 6: *Solanum nodiflorum* +; in number 7: *Marchantia* sp. 3.3; in number 11: *Cyperus virens* subsp. *drummondii* +; in number 12: *Ipomoea* sp. 1.2, *Miconia robinsoniana* +.2, *Asplenium serra* +; in number 14: *Psidium guajava* 3.2, *Pilea* sp. +; in number 18: *Lycopodium reflexum* +; in number 19: *Dichondra repens* 3.3; in number 23: *Rhynchospora rugosa* 2.2.

(Stands 11–13). The former was found in sheltered sites that were free or nearly so from direct southern winds, where shrubs like *Tournefortia rufo-sericea*, *Acnistus ellipticus*, *Psychotria rufipes*, and ferns like *Ctenitis pleiosoros* and *Hypolepis hostilis* were seen.

The first type corresponds closely to van der Werff's (1978) "atypical" community of his table 10, and to Hamann's (1981) *Jaegeria crassa* community (Site 15), although there are some differences in species composition.

14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
680	580	580	620	680	630	730	66	660	690	780	780	670	810	685	720	680	670	680	670
SSE	S		WSW	SE	NNW	—	NNW	NNW	NW	SE	SE	SE	—	NW	NW	—	NW	NW	NE
30	5	5	5	25	15	—	30	30	25	30	30	30	—	20	30	—	25	25	30
12	11	9	12	10	8	4	5	4	9	7	7	6	5	4	5	3	3	3	2
2.2	3.2	4.4	4.4	5.5	5.4	2.2	3.4	4.4	3.3	2.2	4.4	2.2	3.3	3.3	4.4	4.4	3.3	4.3	3.4
3.4	5.4	2.3	4.4	3.3	2.2	5.5	5.5	5.5	4.4	2.3	3.3	5.4	2.3	5.5	2.3	5.5	5.5	5.5	5.5
.	+.2	1.2	+.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	+	+	+	1.1	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.
+.2	+.2	.	+.2	.	+.2	.	.	.	+.2	.	.	.	.	.	.	.	.	.	.
1.2	1.2	2.2	.	.	2.2	.	.	.	.	.	.	2.2	.	.	.	.	.	.	.
.	+.2	+.2	+.2	+.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	+	+.2	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
+	.	.	.	.	.	+	+.2	+.2	1.2	1.2	1.2	2.2	+.2	.	.	.	.	.	.
.	.	.	.	.	.	2.2	.	.	+.2	2.2	2.2	1.2	.	+.2	.	.	.	.	.
.	.	.	.	.	.	.	+	+	+.2	.	.	.	4.4	.	2.3	.	.	.	.
.	+	+.2	.	2.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	2.2	.	.	.	.	+	.	.	+	+	.
+.2	+	+	.	1.2	+.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	1.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	.	+.2	.	.	.	.	.	.
3.4	.	.	.	.	.	.	.	.	3.3	.	.	.	.	.	.	.	.	.	.
1.2	.	.	.	.	.	.	.	.	.	2.2	2.2	.	.	.	.	.	.	.	.
.	.	.	2.2	.	.	.	.	.	.	.	.	.	.	.	2.3	.	.	.	.
.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	1.2	.	+.2	+.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	(+)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
+.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1.2	.	.	.
.	.	.	.	.	1.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
2.2	.	.	.	.	.	.	.	.	.	1.2	+.2	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4.4	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	+.2	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	2.2	3.3	.	.	.	.	.	.	.	.

PTERIDIUM AQUILINUM/BLECHNUM POLYPODIOIDES COMMUNITY

The *Pteridium aquilinum/Blechnum polypodioides* community (Table 2) occupied the largest area of the highland slopes. It was widely distributed on the south- and north-facing slopes (Fig. 2B). The vegetation was low on south-facing slopes, one meter high on north-facing slopes. *Paspalum conjugatum* was rare here; *Phyllanthus caroliniensis* and *Hypericum uliginosum* were frequent.

The community is divided into two types. One is characterized by the presence of *Vigna luteola*, *Conyza bonariensis*, *Pityrogramma calomelanos*, *Jaegeria gracilis*, and *Thelypteris pilosula*

TABLE 3. *Lycopodium clavatum* community.

Stand number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Altitude (m)	720	700	710	720	710	710	810	670	625	730	800	720	720	620	630	580	680	730	690
Slope aspect	SE	SE	SE	SE	SE	SE	SSE	SE	SSE	ESE	SE	SE	SE	SE	SSE	ENE	ESE	SE	SSE
Slope (degrees)	30	30	27	27	25	25	25	30	35	30	20	30	30	30	35	15	20	—	30
Numbers of species	9	12	9	7	9	8	12	8	11	9	11	7	4	6	9	8	8	6	11
CHARACTERISTIC SPECIES																			
Lycopodium clavatum	5.4	4.4	4.4	3.4	5.4	5.4	4.4	5.5	4.4	5.4	5.5	5.4	5.4	5.4	5.4	5.5	5.5	3.4	5.4
DIFFERENTIAL SPECIES																			
Hypericum uliginosum	+.2	.	1.2	2.2	+	+.2	3.3	1.2	+.2	1.2	+	.	.	.	.	.	.	.	.
Nephrolepis cordifolia	+	(+)	+.2	1.2	.	.	2.2	+.2	3.2	1.2	+	.	.	.	.	+.2	.	.	.
Polypodium tridens	1.2	1.2	1.2	2.2	(+)	1.2	.	.	.	.	.	.	.	.	.	.	.	.	.
COMPANIONS																			
Pteridium aquilinum	1.2	3.3	2.2	2.3	1.1	1.1	1.1	.	1.1	2.2	1.2	1.2	2.2	1.2	1.1	1.1	1.1	1.1	2.1
Blechnum polypodioides	.	(+)	2.3	1.2	(+)	+.2	2.2	+.2	2.3	3.3	2.2	+.2	.	3.4	2.2	+.2	1.2	.	1.2
Phyllanthus caroliniensis	1.2	1.2	1.2	.	1.2	1.2	+.2	+	.	1.2	1.1	3.3	1.2	.	+	.	+	.	+
Vigna luteola	1.2	3.2	.	.	.	.	+	.	(+)	.	.	1.2	2.2	+.2	+. 2	+.2	.	.	.
(Brown hepatics)	.	.	3.3	.	3.3	4.4	.	.	.	1.2	+.2	.	.	.	.	.	.	4.4	2.2
Commelina diffusa	+	+.2	.	.	.	.	+.2	.	.	+	.	.	.	.	.	+.2	.	.	+.2
Thelypteris pilosula	.	.	.	.	.	.	.	+.2	+.2	.	.	.	.	+.2	+.2	+. 2	.	.	+.2
Pityrogramma calomelanos	.	.	.	.	.	.	.	+.2	(+)	.	+	.	.	.	.	.	1.2	.	.
Borreria laevis	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	(+)	+.2	.	.
Justicia galapagana	.	.	.	.	1.2	2.2	.	.	(+)	.	.	.	.	.	.	.	.	.	.
Lycopodium cernuum	.	.	.	.	1.2	.	1.2	.	.	(+)	.	.	.	.	.	.	.	.	.
Cyathea weatherbyana	.	.	.	.	.	.	1.2	.	.	.	.	.	.	.	.	.	.	1.1	+
Miconia robinsoniana	.	.	.	.	.	.	.	.	1.2	.	.	.	.	1.2	+.2	.	.	.	.
Alternanthera halimifolia	(+)	.	.	.	.	.	.	.	.	.	.	1.2	.	.	.	.	.	.	.
Blechnum occidentale	.	(+)	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.
Panicum dichotomiflorum	.	.	1.2	1.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Centella asiatica	.	.	.	.	.	.	2.3	.	.	.	.	.	.	.	.	.	.	.	3.3
Polypodium aureum	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	.	.	.	.
Cyperus grandifolius	.	.	.	.	.	.	.	.	(+)	.	.	.	.	.	.	.	+	.	.
Asplenium serra	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	1.1	.

Other companions. In stand number 2: *Cissampelos pareira* +.2, *Drymaria cordata* +; in number 7: *Peperomia* spp. +; in number 11: *Ophioglossum reticulatum* +, Gramineae sp. +; in number 15: *Polypodium Hydrocotyle* sp. +.

TABLE 4. *Hypericum uliginosum* community and *Polypodium tridens* community.

Stand number	1	2	3	4	5	6	7	8	9	10
Altitude (m)	670	670	670	660	570	580	670	690	760	760
Slope asepct	SSE	SSE	SSE	—	—	—	—	—	—	—
Slope (degrees)	30	3	2	—	—	—	—	—	—	—
Numbers of species	8	4	4	5	6	3	5	3	3	4
DOMINANT AND CHARACTERISTIC SPECIES										
Hypericum uliginosum	4.3	3.3	4.4	3.3	+.2	2.2	1.2	2.2	3.2	3.2
Polypodium tridens	.	.	.	.	3.3	4.3	5.4	2.3	3.3	3.3
(Brown hepatics)	.	.	.	.	2.2	.	+	2.2	.	2.2
COMPANIONS										
Cladonia spp.	1.2	2.3	.	.	.	2.2	+	.	.	.
Stenotaphrum secundatum	.	.	2.2	2.2	.	.	.	.	1.2	2.2
Jaegeria gracilis	.	1.2	2.3	2.2	.	.	.	.	.	.
Rhynchospora rugosa	.	.	2.3	1.2	.	.	.	.	.	.
Pteridium aquilinum	.	.	.	.	1.2	.	1.2	.	.	.

Other companions. In stand number 1: *Conyza bonariensis* +, *Blechnum polypodioides* 1.2, *Phyllanthus caroliniensis* +.2, *Hypoxis decumbens* 2.2, *Histiopteris incisa* +, *Dicranopteris flexuosa* +; in number 2: *Paspalum* sp. 2.2; in number 4: *Setaria geniculata* 2.2; *Pityrogramma calomelanos* 1.2, *Cladina* spp. 2.2.

(Stands 1–19 in Table 2), and the other by their absence (Stands 20–33), although there are exceptions. The first type closely resembles Hamann's (1981) *Pteridium aquilinum-Jaegeria gracilis* community (Site 19).

LYCOPODIUM CLAVATUM COMMUNITY

The *Lycopodium clavatum* community (Table 3) was distributed mostly on south-facing slopes in low and middle altitudes of the highland (Fig. 2C). The slopes are directly exposed to southern winds and sometimes dried by them, as in the dry period February–April 1970, but moistened by moisture-saturated winds on foggy and rainy days. The habitat fluctuates between dry and wet extremes.

The dominant species was always *Lycopodium clavatum*, associated with *Pteridium aquilinum* and *Blechnum polypodioides*. Major companions in the community were *Phyllanthus caroliniensis*, *Vigna luteola*, and *Commelina diffusa*. Small patches of brown hepatics (Tables 2–5), probably *Jungermanniales* species, were frequently prominent in the *Lycopodium clavatum* community.

This community is subdivided into two types. One type (Stands 1–11 in Table 3) is characterized by *Hypericum uliginosum*, *Nephrolepis cordifolia*, and *Polypodium tridens*, and the other by their absence (Stands 12–19).

HYPERICUM ULIGINOSUM COMMUNITY

Figure 2D shows the distribution of the *Hypericum uliginosum* community on slopes at rather low altitudes. The community was some 30 cm tall and was found only on thin soils, which were dry on fine days.

POLYPODIUM TRIDENS COMMUNITY

The *Polypodium tridens* community (Stands 5–10 in Table 4) was found on thin soils accumulated on nearly exposed lava (Fig. 2E). Here again, *Hypericum uliginosum* was always found. The

TABLE 5. *Pernettya howellii* community.

Stand number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Altitude (m)	790	800	790	790	790	790	730	810	780	810	790	780	810	810	810	800	810	740	670	740	740	740
Slope aspect	SE	SSE	SE	SE	SE	SE	SE	SE	ESE	SE	SSE	ESE	SW	SSE	SSE	SE	NNE	SE	SE	SE	SE	SE
Slope (degrees)	30	35	35	35	35	30	30	27	35	27	35	35	45	30	27	27	20	30	80	30	30	30
Numbers of species	6	6	6	4	5	7	5	8	5	7	8	5	8	5	7	8	9	3	3	3	2	2
CHARACTERISTIC SPECIES																						
Pernettya howellii	5.5	3.3	4.4	5.4	4.4	5.5	5.5	5.4	5.4	5.4	5.5	5.4	5.4	5.5	5.4	4.4	5.4	5.5	5.5	5.5	5.5	5.5
DIFFERENTIAL SPECIES																						
Hypericum uliginosum	1.2	.	+	+	2.2	1.2	1.2	2.2	1.2	1.2	1.2	1.2	+	(+)	1.2	+.2	(+)	.	.	.	.	.
Pteridium aquilinum	1.1	+.2	.	.	.	+	1.1	+	+	1.2	.	1.2	+	1. 1	1.1	(+)	2.2	+	.	1.1	.	.
Nephrolepis cordifolia	.	.	2.3	+	2.2	+	.	+.2	.	1.2	.	.	.	2.3	2.2	.	1.2	.	+	.	.	.
Phyllanthus caroliniensis	+.2	2.2	+.2	.	.	.	.	+.2	.	2.2	1.2	.	1.2	.	1.2	(+)	+.2	.	.	.	.	.
(Brown hepatics)	2.2	.	.	.	1.2	2.2	2.2	.	.	.	1.2	.	+.2	.	.	.	+.2	.	.	.	.	.
COMPANIONS																						
Blechnum polypodioides	1.2	3.3	4.4	2.3	1.2	+.2	.	2.2	3.3	2.2	1.2	1.2	3.2	2.3	2.2	4.4	3.2	1.2	2.1	2.2	1.2	1.2
Commelina diffusa	.	.	.	.	.	.	.	1.2	.	.	.	.	.	.	1.2	+	+	.	.	.	.	.
Vigna luteola	.	.	.	.	.	.	.	.	+.2	+	.	.	.	.	.	.	+	.	.	.	.	.
Conyza bonariensis	.	+	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.
Histiopteris incisa	.	1.2	(+)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lycopodium reflexum	.	.	.	.	.	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Thelypteris pilosula	.	.	.	.	.	.	.	.	.	.	.	+	+.2	.	.	.	.	.	.	.	.	.

Other companions. In stand number 7: *Stenotaphrum secundatum* + .2; in number 8: *Cyathea weatherbyana* + .2; in number 11: *Pityrogramma calomelanos* + .2; in number 16: *Hyptis rhomboidea* + , *Panicum dichotomiflorum* + .2.

habitat was dry and, therefore, the number of component species was small (only 4.0 on average in this community).

PERNETTYA HOWELLII COMMUNITY

This ericaceous community (Table 5) was nearly exclusively distributed on southeast-facing windward slopes in high altitudes in the highlands (Fig. 2F). The largest tract of the community is 10 m wide and 30 m long on a south-facing, inside steep slope of a crater west of the highest point of Mt. Crocker. The habitat was extremely dry February–April, 1970. The *Pernettya howellii*

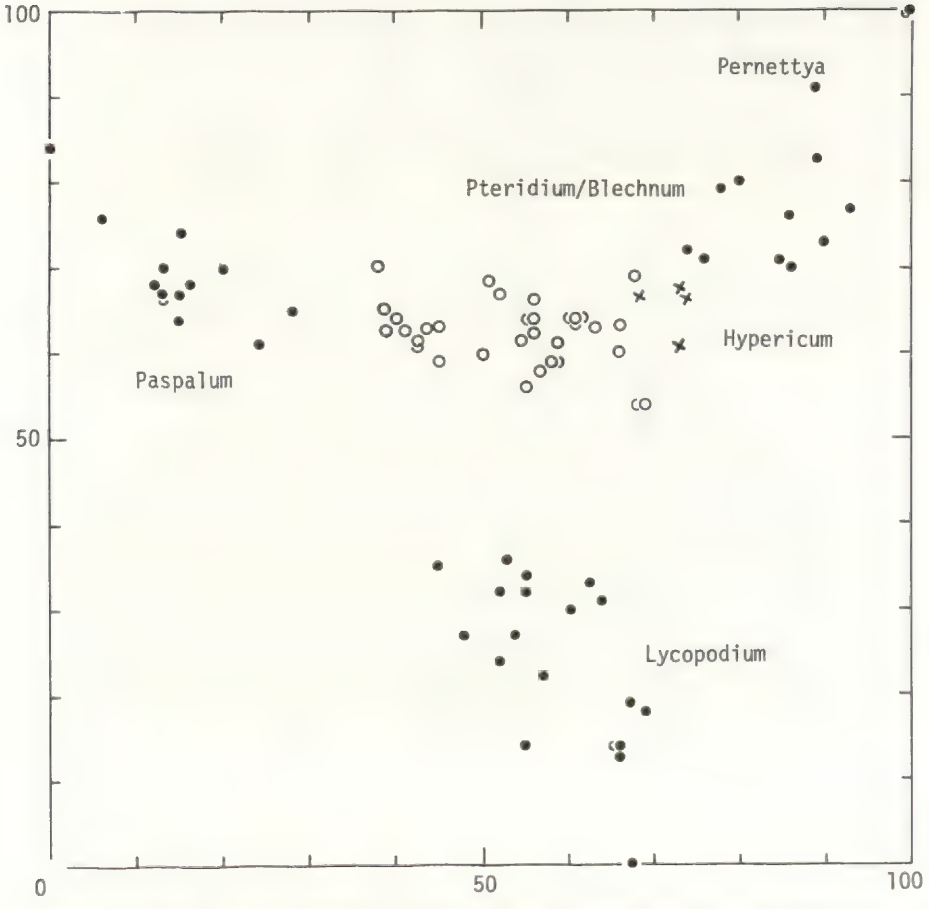

FIGURE 1. Scatter diagram of vegetation samples (excluding six *Polypodium tridens*-dominated stands), processed by reciprocal averaging.

community was about 30 cm high and consisted of a limited number of species (5.5 species on average). *Blechnum polypodioides* was an important companion in the community.

This community can be divided into two types. One is characterized by the presence of *Hypericum uliginosum, Pteridium aquilinum, Nephrolepis cordifolia, Phyllanthus caroliniensis,* and brown liverworts (probably *Jungermanniales* species as in the *Lycopodium* community) (Stands 1–17 in Table 5), and the other is distinguished by their absence (Stands 18–22), although there are three exceptional occurrences.

Van der Werff (1978) described a stand dominated by *Pernettya howellii,* which was found on a "wind-exposed slope." The area could be the same that I studied in 1970 (Stands 13–16 in Table 5), although the component species are fewer in the present study than in van der Werff's (1978). The difference must be due to the difference in quadrat sizes used and the extremely dry conditions in 1970; that year the *Pernettya howellii* community was the driest of the highland communities I studied. However, in 1978 and 1986, I revisited the locality and found that the community was humid by the southern winds, as van der Werff (1978) observed.

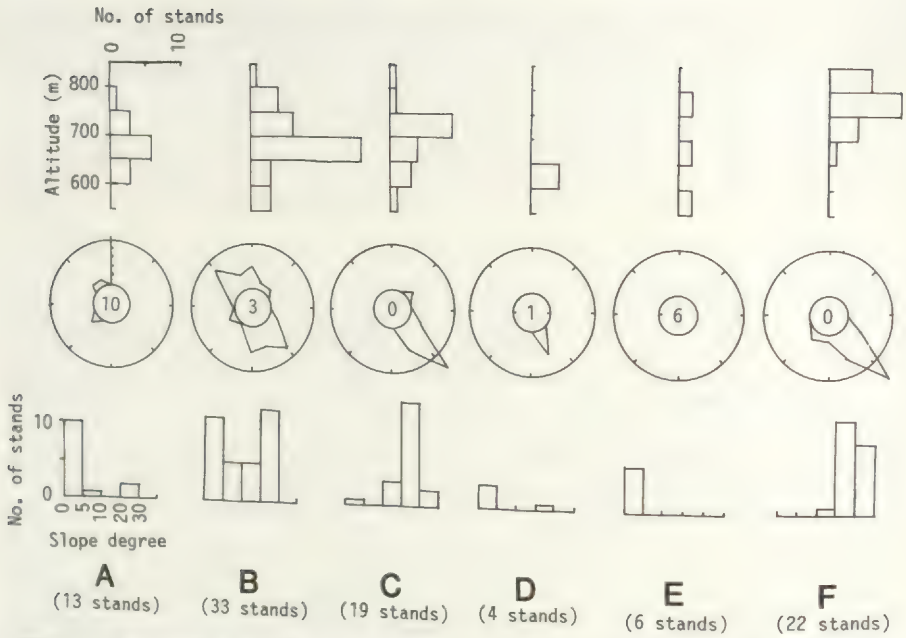

FIGURE 2. Distributions of the recognized communities in relation to altitude (top), slope direction (middle), and slope degree (bottom).—A. *Paspalum conjugatum* community.—B. *Pteridium aquilinum/Blechnum polypodioides* community.—C. *Lycopodium clavatum* community.—D. *Hypericum uliginosum* community.—E. *Polypodium tridens* community.—F. *Pernettya howellii* community. Numerals in the circles show numbers of relevés sampled from flat topography.

DISCUSSION

Figure 3 illustrates the distribution of the plant communities recognized in the summit area of Santa Cruz, including fens and bogs (described in Itow & Weber, 1974), *Miconia robinsoniana* scrub on the southern slope, and *Scalesia pedunculata* forest on the northern slope.

Van der Werff (1978) described Habenario-Trisetetum howellii from the highlands and listed as the character species *Habenaria monorrhiza, Centella asiatica, Mildella intramarginalis, Scleria hirtella, Setaria geniculata, Stenotaphrum secundatum,* and *Trisetum howellii*. Since the quadrat size used is larger in van der Werff's (1978) study than in mine, the number of species listed in a sample (relevé) is correspondingly higher. Despite this difference, the vegetation described in Tables 1–4 corresponds to van der Werff's Habenario-Trisetetum howellii. The most pronounced difference between them is the absence of *Habenaria monorrhiza, Mildella intramarginalis,* and *Trisetum howellii* in the communities described here. The first two species, however, were collected in the highlands in 1970 but did not occur in the sample sites. The third species was neither seen nor collected in 1970. Several sterile specimens of Gramineae, however, turned up in sample sites and were listed as Gramineae spp., as seen in Tables 2, 3, and 4. They might include *Trisetum howellii*. The three species mentioned were rarely seen in the highland vegetation in 1970, possibly due to the extreme dryness in that year.

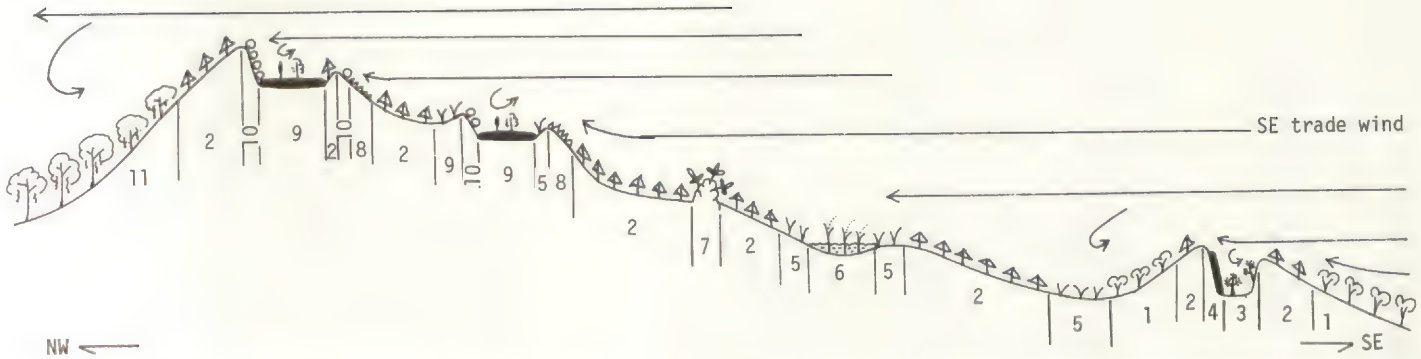

FIGURE 3. Community distribution in the Santa Cruz highland. 1, *Miconia robinsoniana* scrub. 2, *Pteridium aquilinum/Blechnum polypodioides* community. 3, *Cyathea weatherbyana* stand. 4, vertical bog. 5, *Paspalum conjugatum* community. 6, fen. 7, *Polypodium tridens* community. 8, *Lycopodium clavatum* community. 9, raised bog. 10, *Pernettya howellii* community. 11, *Scalesia pedunculata* forest.

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UNDISTURBED VEGETATION ON FERNANDINA, 1964

F. R. Fosberg[1]

Abstract

A description is presented of the vegetation observed in 1964 of an area of a'a lava and pumice at mid elevations on the western slope of Fernandina Island, with a list of species collected. The vegetation on the lava was a sparse or open scrub and scrub forest, that on the pumice field was a bunchy grassland with scattered shrubs. This vegetation was destroyed by a mudflow during the 1968 caldera eruption. Data are presented on the revegetation of the ash bed resulting from the mudflow, contributed by Dr. Dagmar Werner, with a list of plant species observed by her.

Fernandina (Narborough) Island is the most active volcano in the Galápagos Archipelago, known to have erupted eight times in the last 23 years, since 1964, when the notes on which this account is based were made. Since explosive eruptive activity or lava flows often result in drastic changes in vegetation, any account made at a fixed point in time has historical value in understanding vegetation dynamics. Hence, since I had a unique opportunity to study lower mid-elevation vegetation on pumice and a'a lava on the west slope of Fernandina in February 1964, it seems worthwhile, even after 23 years, to try to picture, from my notes made then, the vegetation of a single small area. I have been told that subsequent ash falls have, since 1964, modified the situation I am attempting to portray. I only regret that the limited time I had available did not permit even a cursory description of the entire extent of the strip of vegetation studied, from the sea to the summit of the volcano. What is possible from notes made then is a more detailed, but still only reconnaissance account, of a small area, perhaps less than a square kilometer, at about 300–400 m elevation on a strip of fairly old surface, between younger lava flows.

The Occasion

The occasion was during the University of California Expedition in 1964, when Dr. John Hendrickson attempted to rediscover the lost Narborough tortoise, found only once, by Rollo H. Beck in 1906. It was thought, possibly incorrectly, that this fairly wide strip of vegetation was the most likely place that this animal might persist. A small party of two herpetologists, one young and vigorous general naturalist and superb observer, and one somewhat over-mature botanist-ecologist, was deposited at what seemed a reasonable elevation for tortoises and left for three days to look for the tortoises and make general observations and collections. The roughness of the terrain and the complexity of the patterns were such that three days was an inadequate period to take full advantage of this opportunity. Due to lack of equipment for preservation, promised by the promoters of the expedition, the plant collections did not all reach Washington in good condition, some being beyond recovery. These observations, therefore, are not as completely or adequately documented as could be desired. The specimens, such as they are, are deposited in the U.S. National Herbarium, Smithsonian Institution.

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Monogr. Syst. Bot. Missouri Bot. Gard. 32: 59–66. 1990.

The Site of Observations

The general landscape of Fernandina is of lava flows of various ages and textures radiating out from the main volcano and large areas covered by ash and pumice. The main aspect is of a mosaic of blacks, browns, areas of thin green, and small, green, well-vegetated *kipukas* or pockets of older soil missed by recent flows. These would be well worth investigating, but we only saw them from the air. The single complete strip of green on the southwest slope, extending from the sea to the summit, was where we were put down, between 300 and 400 m elevation. The general surface was of an old and somewhat weathered, vegetated a'a or rough lava, with a large strip and smaller patches of light-colored pumice, from sand-sized to large-pebble-sized rough fragments. On the west side was a small spatter-cone, the scoria merging with the a'a lava. Farther away were flows of bare pahoehoe, or smooth to ropy lava, almost lacking vegetation.

The Vegetation in 1964

The vegetation on the prevailing a'a lava was a sparse shrub and herb layer with scattered trees of *Bursera graveolens* and *Zanthoxylum fagara*, more closely spaced in low places, and especially more abundant near the base of the small cone. Between and under the trees were the sparse scrub *Psychotria rufipes, Scalesia affinis, Cordia leucophlyctis, Solanum erianthum, Lippia rosmarinifolia*, and *Macraea laricifolia;* and many herbs, including *Pilea baueri, Laportea aestuans, Setaria setosa, Solanum* (*Lycopersicon*) *cheesmaniae*, and *Acalypha parvula*.

The spatter-cone is partially bare, spottily covered by apparently fresh fine pumice. A scrub of scarcely branched *Macraea laricifolia, Waltheria ovata, Chiococca alba, Cordia revoluta, Gossypium darwinii, Lippia rosmarinifolia, Zanthoxylum fagara, Froelichia nudicaulis*, and a few *Jasminocereus* can be found. An assortment of herbs are found on the slopes between the shrubs, including *Aristida repens, Mollugo snodgrassii, Cyperus aristatus, Lobelia xalapensis, Cenchrus platyacanthus, Galactea velutina, Chrysanthellum pusillum, Spermacoce ericifolia*, and a single individual of *Sonchus oleracea*, the only undoubted exotic seen in the whole area. On the rim of the small crater of the cone are *Blainvallea dichotoma* and *Salvia occidentalis; Bursera graveolens* is in the crater.

The most distinctive vegetation is a grassland on the large pumice field where we were camped. The commonest grasses were *Bouteloua disticha* and *Paspalum galapageium*, with some *Aristida repens, Cenchrus platyacantha*, and *Setaria setosa*. Many broad-leafed herbs are scattered in the grass (see list below) as well as scattered shrubs of *Macraea laricifolia, Zanthoxylum fagara, Psidium galapageium, Psychotria rufipes, Waltheria ovata, Chiococca alba, Lippia rosmarinifolia*, and *Opuntia insularis*. One plant of the *Opuntia* had a large bite taken out of one pad, well above the probable reach of the land iguanas. Large droppings were also seen that may well have been from tortoises that must have bitten the piece out of the *Opuntia*. But no tortoises were seen in all the days of searching for them. Land iguanas, dull salmon in color, inhabited this grassland, made their burrows in the pumice, and sunned themselves in small bare places.

The vegetation of the area is not at all homogeneous, varying much locally, but it can be grossly divided into two assemblages, that on the pumice fields, and that on a'a lava. The lava had pockets of pumice in cavities and depressions, which may well have been the habitat of some plants that would not have survived on the lava otherwise. Some of the smaller herbs, especially ferns, such as *Adiantum, Doryopteris, Notholaena, Asplenium pumilum*, and *Polypodium tridens*, seemed to occur particularly in crevices and cavities in rocks, both in a'a areas and on small lava outcrops from the pumice. Some plants, such as *Psychotria rufipes*, occurred mostly in the shade of larger shrubs or small trees. *Cuscuta gymnocarpa* and *Phoradendron henslovii* are parasites. The *Cuscuta* parasitized herbs and shrubs, the *Phoradendron* trees and large shrubs.

TABLE 1. Plant species found on a'a lava in area studied.

Adiantum concinnum	*Sida spinosa*
Asplenium pumilum	*Waltheria ovata*
Doryopteris concolor	*Passiflora suberosa*
Notholaena galapagensis	*Jasminocereus thouarsii*
Polypodium dispersum	*Sarcostemma angustissima*
Polypodium tridens	*Ipomoea alba?*
Trachypteris pinnata	*Cordia leucophlyctis*
Aristida repens	*Cordia revoluta*
Cenchrus platyacanthus	*Heliotropium angiospermum*
Paspalum galapageium	*Tournefortia pubescens*
Setaria setosa	*Lippia rosmarinifolia*
Cyperus anderssonii	*Salvia occidentalis*
Commelina diffusa	*Acnistus ellipticus*
Phoradendron henslovii	*Physalis pubescens*
Laportea aestuans	*Solanum cheesmaniae*
Pilea baueri	*Solanum erianthum*
Froelichia nudicaulis var. *lanigera*	*Chiococca alba*
Mollugo snodgrassii	*Psychotria rufipes*
Galactia striata	*Spermacoce ericifolia*
Rhynchosia minima	*Lobelia xalapensis*
Zanthoxylum fagara	*Baccharis gnidiifolia*
Bursera graveolens	*Blainvillea dichotoma*
Acalypha parvula	*Brickellia diffusa*
Croton scouleri	*Chrysanthellum pusillum*
Phyllanthus carolinensis	*Darwiniothamnus tenuifolius*
Gossypium darwinii	*Scalesia affinis*
Sida hederifolia	*Sonchus oleraceus*

The grassy vegetation on the pumice was rather bunchy, with openings between the tufts frequently occupied by mats of *Rhynchosia minima* and *Alternanthera filifolia*.

POST-ERUPTION VEGETATION

After the above was written, Dr. Dagmar Werner, herpetologist at the Smithsonian Tropical Research Institute, Balboa, Panama, kindly sent me information on the subsequent history of the area described above. She spent some months in 1976–1979 at approximately the same locality, studying the behavior of a population of land iguanas (*Conolophus sub-cristatus*). Her study area F270 is located in the area described above and is a rectangle 200 × 160 m, much smaller than the area studied by me.

In 1968, between the times of my visit and hers, the vegetation of the area was destroyed by a mudflow from Fernandina volcano. A layer of ash was deposited on the whole area, which became revegetated by the time of Dr. Werner's study. Some details of the environment and a small vegetation sketch map are published in Werner (1982).

Judging by the information in this publication, the vegetation of the ash surface is now more of an open to sparse scrub, rather than the grassland with scattered shrubs that existed on the pumice field in 1964. Thus the environments and vegetation from which the 1964 and 1976–1979 floras were collected are not strictly comparable. The differing sizes of the areas studied increases the lack of comparability. However, for what they may be worth, the gross floristic statistics in Table 4 are offered.

TABLE 2. Plant species found on pumice in area studied.

Cheilanthes microphylla	*Acalypha parvula*
Aristida repens	*Phyllanthus carolinensis*
Bouteloua disticha	*Waltheria ovata*
Cenchrus platyacanthus	*Passiflora suberosa*
Paspalum galapageium	*Psidium galapageium*
Setaria setosa	*Opuntia insularis*
Cyperus anderssonii	*Cuscuta gymnocarpa*
Cyperus aristatus	*Ipomoea triloba*
Cyperus ligularis	*Cordia revoluta*
Alternanthera filifolia	*Lippia rosmarinifolia*
Cissampelos pareira	*Salvia occidentalis*
Cassia picta	*Psychotria rufipes*
Crotalaria incana	*Spermacoce ericifolia*
Rhynchosia minima	*Bidens riparia?*
Tephrosia decumbens	*Blainvillea dichotoma*
Vigna luteola	*Chrysanthellum pusillum*
Zanthoxylum fagara	*Macraea laricifolia*
Bursera graveolens	

A number of 20 × 20 m-quadrats were laid out, mapped, and observed repeatedly by Dr. Werner who may publish detailed data and analyses of these later.

The species listed by Dr. Werner (pers. comm., 1987), appear in Table 5, with names adjusted to conform with Wiggins & Porter (1971) and later mostly unpublished work.

There is no indication in the material received from Dr. Werner of any herbarium specimen vouchers for these records, so the several new island records should not be considered firm additions to the Fernandina flora. Several species names used by her are not names listed by Wiggins & Porter. Since in all of these cases the genera are represented under other names, such other names have been used because this seemed preferable to introducing names into the list that are not supported by specimens.

OTHER STUDIES OF FERNANDINA VEGETATION

Several descriptions of Fernandina vegetation and accounts of Fernandina flora have been published, one of pre-1968 eruption (Eliasson, 1972) and several post eruption (Hamann, 1981; Hendrix, 1981; Hendrix & Smith, 1986). These have been studied, seeking information bearing on the vegetation in 1964 and 1976–1979, possibly aiding in understanding the changes observed to have occurred between the two times mentioned in this paper. Since these published papers dealt primarily with vegetation of the caldera and caldera rim, and to some extent with the northern and eastern bare lava slopes, there was little of relevance to the mid-elevation *kipuka* vegetation described here.

One striking difference stands out between the flora listed in 1964 and that Hendrix described in her post-eruption successions on the caldera rim. This was the prevalence of "weedy" species in Hendrix descriptions compared with the practical absence of such in the 1964 lists. It is not clear how much of this difference is due to different concepts of weeds and weediness. I suppose that most pioneer species capable of establishing and persisting on fresh lava and pumice might be called weeds. In 1964 I referred only to the undoubted exotic, *Sonchus oleraceus*, of which one individual was seen, as a weed. This species was abundant in the caldera-rim vegetation in 1976–1979.

No comment would be of great significance on similarities or difference between the vegetation on two or three isolated and geographically different sites. My sole purpose in this paper is to place

TABLE 3. Plant species collected on area studied. All collections by Fosberg; collection numbers in parentheses. Specimens in US if retained.

POLYPODIACEAE
Adiantum concinnum Hook. & Arn. (*44999*)
Asplenium pumilum Sw. (*44998, 45013*)
Cheilanthes microphylla (Sw.) Sw. (*45059*)
Doryopteris concolor (Langsd. & Fisch.) Kunth (*44987*)
Notholaena galapagensis Weatherby (*45016, 45065*)
Polypodium dispersum O. M. Evans (*45078*)
Polypodium tridens Kunze (*44996, 45001, 45097*)
Trachypteris pinnata (Hook. f.) C. Chr. (*45074*)
POACEAE (Gramineae)
Aristida repens Trin. (*45021*)
Bouteloua disticha (HBK) Benth. (*45052*)
? *Cenchrus platyacanthus* Andersson (*45037, 45048*)
Paspalum galapageium Chase (*45008, 45018*)
Setaria setosa (Sw.) P. Beauv. (*45054*)
CYPERACEAE
Cyperus anderssonii Boeckeler (*44984, 45044, 45077*)
Cyperus aristatus Rottb. (*44985, 45032, 45047*)
Cyperus ligularis L. (*45045*)
COMMELINACEAE
Commelina diffusa Burm. f. (*45003, 45079*)
VISCACEAE
Phoradendron henslovii (Hook. f.) Robinson (*44979, 45075, 45085, 45093, 45094*)
URTICACEAE
Laportea aestuans (L.) Chew (*44986*)
Pilea baueri Robinson (*45005*)
AMARANTHACEAE
Alternanthera filifolia (Hook. f.) Howell (*45093*)
Froelichia nudicaulis var. *lanigera* (Anderson) Eliasson (*45006, 45029*)
MOLLUGINACEAE
Mollugo snodgrassii Robinson (*45091*)
MENISPERMACEAE
Cissampelos pareira L. (*45062, 45063*)
FABACEAE (Leguminosae)
Cassia picta Don (*44995*)
Crotalaria incana L. (*45051*)
? *Galactia striata* (Jacq.) Urban (*45038, 45086*)
Rhynchosia minima (L.) DC. (*45058*)
Tephrosia decumbens Benth. (*45061*)
Vigna luteola (Jacq.) Benth. (*45087*)
RUTACEAE
Zanthoxylum fagara L. (*45027*)
BURSERACEAE
Bursera graveolens (HBK) Triana & Planch. (*45080*)
EUPHORBIACEAE
Acalypha parvula Hook. f. (*44981, 44991*)
Croton scouleri Hook. f. (*44980, 44992, 45068*)
Phyllanthus carolinensis Walter (*44988, 45082*)
SAPINDACEAE
Dodonaea viscosa var. *spatulata* (Smith) Benth. (*45084*)
MALVACEAE
Gossypium darwinii Watt (*45037*)
Sida hederifolia Cav. (*44997*)
Sida spinosa L. (*45081*)
STERCULIACEAE
Waltheria ovata Cav. (*45028*)
PASSIFLORACEAE
Passiflora suberosa L. (*45002, 45064*)
MYRTACEAE
Psidium galapageium Hook. f. (*45097*)
CACTACEAE
Opuntia insularis Stewart (*45083*)
ASCLEPIADACEAE
Sarcostemma angustissima (Andersson) Holm (*45017, 45098*)
CONVOLVULACEAE
Cuscuta gymnocarpa Engelm. (*45043, 45055*)
Ipomoea alba L.? (*45022*)
Ipomoea triloba L. (*45049*)
BORAGINACEAE
Cordia leucophlyctis Hook. f. (*45011, 45072*)
Cordia revoluta Hook. f. (*45030, 45099*)
Heliotropium angiospermum Murray (*44990*)
Tournefortia pubescens Hook. f. (*44982, 45069, 45071*)
VERBENACEAE
Lippia rosmarinifolia Andersson (*45014, 45039, 45067*)
LAMIACEAE (Labiatae)
Salvia occidentalis L. (*45040, 45050*)
SOLANACEAE
Acnistus ellipticus Hook. f. (*45073, 45015*)
Physalis pubescens L. (*45066*)
Solanum cheesmaniae (Riley) Fosb. *Lycopersicon cheesmanii* Riley (*45012*) [for nomenclatural clarification see Kew Bull. 62: 181. 1987.]
Solanum erianthum D. Don (*45010*)
RUBIACEAE
Chiococca alba (L.) S. F. Blake (*45000, 45026, 45046*)
Psychotria rufipes Hook. f. (*45009*)
Spermacoce ericifolia (Hook. f.) Fosb. *Borreria ericifolia* Hook. f. (*45007, 45024, 45019, 45090*)
CAMPANULACEAE
Lobelia xalapensis HBK (*45033*)
ASTERACEAE (Compositae)
Baccharis gnidiifolia HBK (*45075*)
Bidens riparia HBK ? (*45056*)
Blainvillea dichotoma (Murray) Stewart (*45031, 45060*)
Brickellia diffusa (Vahl) A. Gray (*45004*)
Chrysanthellum pusillum Hook. f. (*45041*)
Darwiniothamnus tenuifolius (Hook. f.) Harling (*45034*)
Macraea laricifolia Hook. f. (*45042, 45096*)
Scalesia affinis Hook. f. (*4520*)
Sonchus oleraceus L. (*45033*)

TABLE 4. Comparison of 1964 vegetation with that of 1976–1979.

Total flora observed in 1964	71 species
Of these, also observed in 1976–1979	49 species
Not found in 1976–1979	22 species
Total species observed in 1976–1979	80 species
Of these, also observed in 1964	49 species
Not found in 1964	31 species

TABLE 5. List of vascular plant species recorded by Dr. Dagmar I. Werner on Isla Fernandina, Galápagos, 1976–1979.

POLYPODIACEAE
Adiantum concinnum Humb. & Bonpl. ex Willd.
Cheilanthes microphylla (Sw.) Sw.
Doryopteris concolor (Langsd. & Fischer) Kuhn
Notholaena galapagensis Weatherby & Svenson
Polypodium tridens Kunze
Pityrogramma calomelanos (L.) Link
Pityrogramma tatarea (Cav.) Maxon
Pteridium aquilinum (L.) Kuhn
Thelypteris sp.
Trachypteris pinnata (Hook. f.) C. Chr.
POACEAE (Gramineae)
Anthephora hermaphrodita (L.) O. Kuntze
Aristida repens Trin.
Bouteloua disticha (HBK) Benth.
Cenchrus platyacanthus Andersson
Eragrostis ciliaris (L.) R. Br.
Paspalum galapageium Chase
Pennisetum pauperum Nees ex Steudel
Setaria setosa (Sw.) P. Beauv.
Sporobolus indicus (L.) R. Br.
Trichoneura lindleyana (Kunth) F. Ekman
CYPERACEAE
Bulbostylis hirtella (Schrader) Nees ex Urban
Cyperus anderssonii Boeckeler
Cyperus ligularis L.
AMARANTHACEAE
Alternanthera filifolia (Hook. f.) Howell
Froelichia nudicaulis Hook. f.
MOLLUGINACEAE
Mollugo snodgrassii Robinson
MENISPERMACEAE
Cissampelos pareira L.
FABACEAE (Leguminosae)
Crotalaria incana L.
Phaseolus mollis Hook. f.
Rhynchosia minima (L.) DC.
Vigna luteola (Jacq.) Benth.
RUTACEAE
Zanthoxylum fagara L.
BURSERACEAE
Bursera graveolens (HBK) Triana & Planch.
EUPHORBIACEAE
Acalypha parvula Hook. f.
Croton scouleri Hook. f.
Phyllanthus carolinensis Walter
Ricinus communis L.
MALVACEAE
Abutilon depauperatum (Hook. f.) Andersson ex Robinson
Sida salviifolia Presl
STERCULIACEAE
Waltheria ovata Cav.
CACTACEAE
Opuntia insularis Stewart
MYRTACEAE
Psidium galapageium Hook. f.
PLUMBAGINACEAE
Plumbago scandens L.
BORAGINACEAE
Cordia leucophlyctis Hook. f.
Cordia revoluta Hook. f.
Heliotropium angiospermum Murray
Tournefortia psilostachya HBK
Tournefortia rufo-sericea Hook. f.
VERBENACEAE
Lippia rosmarinifolia Andersson
LAMIACEAE (Labiatae)
Hyptis spicigera Lam.
Salvia occidentalis Sw.
SOLANACEAE
Solanum erianthum D. Don
Solanum nigrum L.
RUBIACEAE
Chiococca alba (L.) A. S. Hitchc.
Psychotria rufipes Hook. f.
Spermacoce ericifolia (Hook. f.) Fosb.
CAMPANULACEAE
Lobelia xalapensis HBK
ASTERACEAE (Compositae)
Baccharis gnidiifolia HBK
Brickellia diffusa (Vahl) A. Gray
Conyza bonariensis (L.) Cronq.
Darwiniothamnus tenuifolius (Hook. f.) Harling
Gnaphalium vira-vira Molina
Macraea lancifolia Hook. f.
Scalesia affinis Hook. f.
Sonchus oleracea L.

on record observations on the flora and vegetation of a particular mid-elevation area at two points in time, before and after a major catastrophic change in the environment. Any observations on Fernandina vegetation are of conservation interest as examples of vegetation unaltered by actions of large exotic herbivores, and a general examination, especially of the numerous *kipukas* seen from the air in 1964 but not visited, would be of particular value. Such a study could help in understanding changes due to introduction of exotic plants and animals on islands.

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INTRA-ARCHIPELAGO DISTRIBUTION PATTERNS OF VASCULAR PLANTS IN GALAPAGOS[1]

Henning Adsersen[2]

ABSTRACT

Knowledge of the distribution of organisms in the Galápagos is essential for conservation measures, and for research on diversity and similarity of islands or communities. Most papers on the distributions of Galápagos plants give a biased picture. Based on statistical analysis on updated material, it is shown that the distributions of ferns and allies are random and that the composition is a diluted subset of the neoptropical fern flora. The seed plant flora will probably not show a similar pattern—it is likely that it is possible to define significant groupings based on island flora data. Such units, defined at the island flora level, are open to interpretations that may include chorological, chronological, or ecological elements. On the generic level, the distribution pattern offers hints for understanding of phylogeny within genera with many endemics. This is exemplified with the endemic genera *Lecocarpus, Scalesia,* and *Darwiniothamnus.*

One of the fundamentals in the conservation measures enforced by the Galápagos National Park Service is that the distribution of species among the islands must not be altered by transfer of organisms from one island to another or by impact that leads to extinction of indigenous island populations.

To approach this ambitious goal it is necessary to have thorough knowledge of the natural occurrence of organisms. For the spectacular animals, mapping and census have been performed successfully, but for the plants such exact indications of distribution are scanty.

Gathering and studying distribution data belong within the multidisciplinary field of biogeography. This research area involves many levels of organization: single species or subspecies occurrences, spatial aspects of population changes, community description and localization, ecosystem structure, landscape dynamics, and florulae and faunulae of islands and their relationships to each other and to continental units. The time horizons considered vary from the scale of phenological events to millions of years of evolution and continental drift. Many theories or doctrines have been proposed to account for the observed patterns, and some have gained status as paradigms that have cast new light on phenomena far away from biogeography. Studies on the distribution of Galápagos organisms have been performed at almost any of the levels above, but it is beyond the scope of the present paper to touch on all aspects of plant geography. Emphasis will be on detection of patterns of intra-archipelago distribution and what the detected patterns may imply for island biogeographical interpretations, for recognition of floristic regions within the archipelago, and for assessment of phylogeny within genera with pronounced radiative speciation in Galápagos.

Species distribution maps or similar indication of range are as essential in this research approach as for management but are published infrequently. This is not because botanists or ecologists have shown no interest. Hooker, who was the first to publish monographically on Galápagos plants (1847a, b), emphasized species distribution pattern, mainly based on Darwin's collections. Stewart,

[1]The Charles Darwin Research Station, The Galápagos National Park Service, and their staffs, are thanked for working permits and endless help, hospitality, and friendliness. Dr. H. van der Werff is heartily thanked for Galápagos company and many discussions on ferns and other plants. He generously placed original field data at my disposition. The field studies were supported by Unesco, the Charles Darwin Foundation, the Council for Developmental Research of the Danish Foreign Ministry, the Danish Natural Science Research Council, and Julie von Müllen's Legat, which also financed my participation in the workshop.

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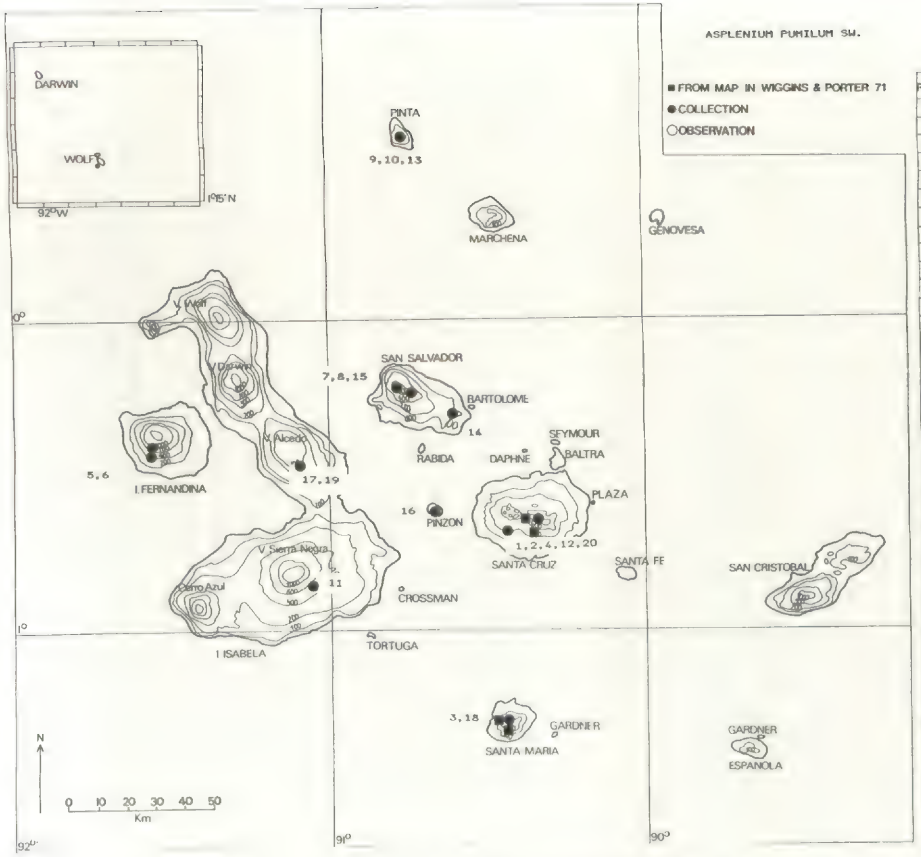
maybe the keenest plant collector visiting the islands, made the first general botanical description and concluded with species lists for each island in 1911. These results were treated by Kroeber (1916), who is the one who is most often referred to as their source, e.g., by the school of island biogeography. The pioneers here, Preston (1962) and MacArthur & Wilson (1967), based their considerations on Kroeber's data. Wiggins & Porter (1971) published "dot" maps of each species, indicating origin of the examined specimens. These maps were not intended to serve as distribution maps, but nevertheless they were used as a base for subsequent revisions of the island biogeography of the Galápagos flora: Johnson & Raven (1973), Simpson (1974), Connor & Simberloff (1978). Van der Werff (1983) supplemented the data with his own plentiful records, but many new island or archipelago records among the around 8,000 collection numbers made by Eliasson, Hamann, Adsersen, and Lawesson have never been considered. This vast material is now compiled in order to produce distribution maps with voucher specimen annotation, but as many collections are unmounted, unarranged, and unidentified, the work is tedious. So far only the pteridophytes have been mapped with citations of the Scandinavian collections. A set is deposited at the CDRS herbarium. Figure 1 shows a sample map. A species checklist (Lawesson et al., 1987) is more accurate than the checklists already published. We estimate that the new checklist accounts for at least 95% of the plants occurring on each of the larger islands or volcanoes, although exceptions exist—Cerro Azul and Volcán Wolf are especially poorly represented.

Distribution Pattern and Island Biogeography of Pteridophytes

The theory of island biogeography states that the potential number of species on any island is determined by an equilibrium between immigration from a species pool and extinction. The important implications of the theory that equilibrium species number increases with area due to reduction of extinction rate and that equilibrium species number decreases with isolation due to reduction of immigration rate have been discussed intensively. The theory has often been severely criticized, sometimes for its simple, almost naïve, rational and more often for its improper use. One merit is that it has generated quantitative evaluations of island floras in terms of species diversity and composition similarity, and it has taught us to envision processes that determine the distribution patterns in quantitative dynamic terms (e.g., immigration rates, extinction rates, turnover rates).

The vascular flora of the Galápagos is probably the most often quoted botanical example within island biogeography, in research papers as the ones cited above and in reviews and textbooks. Most attention has been paid to assessing which interarchipelago features (area, elevation, distance from center, etc.) most strongly influence island species number. Connor & Simberloff (1978) used the distribution pattern in the island biogeographical analysis. They knew that their data from Galápagos were little representative, and they even showed that the best predictor for species numbers was the number of collector trips to each island. They used this as an indication that collection efforts had been incomplete; it could, however, be turned around as a proof that field botanists are clever enough to go to where they expect to collect most plants.

As mentioned above, only the pteridophytes have been mapped in a representative way, so an updated island biogeographical analysis, including distribution pattern, can only be performed for this part of the flora. Apart from this pragmatic reason, there are several ecological reasons to view the pteridophytes separately. Dispersal is a condition for immigration, and with respect to dispersal pteridophytes differ considerably from the vast majority of the spermatophytes. With *Azolla* as the sole exception (omitted from the analysis below), all species have spores 20–100 μm in diameter that belong to the air plankton. Hence for the pteridophytes the ocean is less a barrier than for the seed plants. Porter (1983) showed that all pteridophytes originate from the neotropical area, and that 92% occur in the Andean part. For the seed plants, the corresponding figures are 99% from the Neotropics and 92% from the Andean part. Obviously the pteridophytes and spermatophytes of Galápagos have their species pools in the same area.



Ref	Collector	Col.n.	Date	Deposition	Comments
1	Fagerlind	3190	June 1953	S	
2	do.	3177	do.	S	
3	Eliasson	856	13-12 66	S	
4	Adsersen	379	10-6 74	C,CDS	
5	do.	460	20-6 74	C,CDS	1.isl.rec
6	do.	503	22-6 74	C,CDS	
7	do.	1021	15-10 74	C,CDS	
8	do.	1109	17-10 74	C,CDS	
9	do.	1228	13-11 74	C,CDS	
10	do.	1272	16-11 74	C,CDS	
11	do.	2390	31-7 77	C,CDS	1.isl.rec
12	Hamann	1108	71/72	C	
13	do.	826	71/72	C	
14	do.	2091	71/72	C	1.isl.rec
15	do.	2083	71/72	C	
16	do.	1289	71/72	C	1.isl.rec
17	do.	1902	71/72	C	
18	do.	1471	71/72	C	
19	do.	1818	71/72	C	
20	Weber			CDS 874	
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FIGURE 1. Distribution of *Asplenium pumilum* as read from the standard map. Note how insufficiently the Wiggins & Porter (1971) dot map represents the distribution.

TABLE 1. Species numbers, endemism, and minimum immigration numbers for Galápagos plants. (Data from Tryon & Tryon, 1982, and Lawesson et al., 1987.)

	Pteridophytes	Spermatophytes	Spermatophytes/ Pteridophytes
TROPICAL ANDEAN REGION:			
Number of species	1,500	>60,000	>40
GALÁPAGOS:			
Number of species + subspecies	113	491	4.3
Endemics	7	218	31.1
Percentage endemics	6.2%	44.4%	7.2
Minimum immigration number	113	383	3.4

Table 1 shows estimates of the number of pteridophytes and spermatophytes in the Andean area (Tryon & Tryon, 1982; Lawesson, pers. comm.) and figures on pteridophyte and spermatophyte diversity and endemism (based on Lawesson et al., 1987). The ratio between number of seed plants and number of ferns and allies in Galápagos is much lower than that for the Andean region, indicating that the pteridophytes make it much more readily to Galápagos than the seed plants. The percentage of endemism among pteridophytes is only 6.2%, whereas among the seed plants it is 44.4%, and we observe no radiative speciation in the fern group. This may partly be due to two effects of reduced isolation: immigration of species may be so rapid that empty niches are filled more readily by immigration than by evolution, and repeated invasions of spores from species already in the islands may inhibit speciation by adding "conservative" genetic material to the island populations.

Due to the uniformity of their spores, the pteridophytes constitute a dispersal guild and therefore satisfy one of the often neglected conditions for interpretation of their distribution pattern in terms of equilibrium biogeography. Van der Werff (1983) examined the pteridophyte species numbers and found that elevation of islands was more closely correlated to pteridophyte species numbers than island area was. The ecological requirements of ferns limit the area available to them in Galápagos. Virtually none occur in the arid lowland areas. Correspondingly, the area of the mesic to hydric vegetation of the islands, roughly the area above 200 m elevation, predicts the pteridophyte species number of an island better than island area does (Fig. 2). Due to the relatively regular conic shape of the volcanoes, the area above 200 m will be closely correlated to elevation, so van der Werff's finding of a close correlation between log elevation and log pteridophytes does not contradict the correlation presented in Figure 2.

The distribution pattern of pteridophytes can be examined in several ways. Connor & Simberloff (1978) and Simberloff (1978) suggested setting up null hypotheses for the species distributions based on knowledge of or assumptions on species richness on islands and species abundance. In their most realistic model, they simulated species distribution by a Monte Carlo simulation routine, but it is possible to reach a null hypothesis from the same premises by means of an explicit algorithm (see Appendix I). The necessary conditions are that we consider as given constants the number of islands on which each plant occurs and the number of plant species on each island. This makes it possible to calculate how many species should be in common between each island pair. These figures may be compared with the actual common species numbers by a chi^2-test. In Figure 3 the actual common species numbers are depicted against the expected common species numbers. There is no statistically significant difference between the two sets of numbers, suggesting that the species are distributed at random between the islands.

In another approach we may use the actual numbers of species common to island pairs to calculate the similarity between island pteridophyte floras. The similarity indices calculated may then be investigated in relation to geographical features. In Figure 4, the Sørensen quotient of similarity between island pairs is compared with interisland distance. There is no correlation at all, indicating

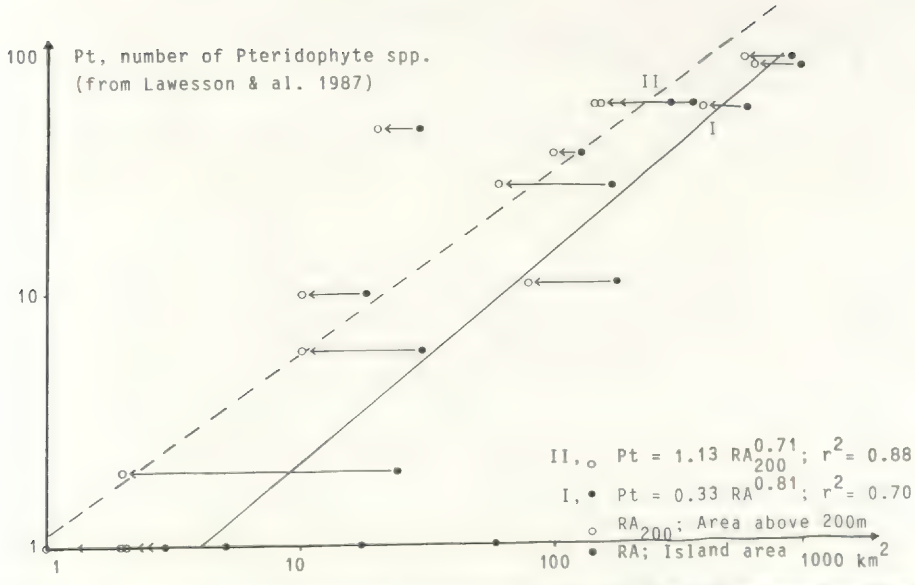

FIGURE 2. Correlation between pteridophyte species number and island area (line I), and area above 200 m (line II). Logarithmic scales.

that neighbor floras may be as mutually different as floras from islands well separated from each other, so there are no great dispersal barriers between the islands. This also points toward a random distribution of pteridophytes.

As indicated in Table 1, immigration contributes far more to the pteridophyte diversity than does evolution. The closest species pool is that of tropical America. Tryon & Tryon's monograph (1982) on tropical American pteridophytes gives a good estimate of this species pool (only 250 of the 3,250 counted species are extratropical). In Figure 5, the numbers of pteridophyte species per family in Galápagos are plotted against the numbers of species per family in the Americas. It was decided to count species per family and not species per tribe or per genus, as there seem to remain many unsettled questions on the subfamiliar levels in fern taxonomy; and it was necessary to dismiss the subfamiliar taxonomy of Morton & Wiggins (in Wiggins & Porter, 1971) in order to perform the analysis. As shown in Figure 5, there is a close correlation between the species/family ratios, suggesting that the isolation effect works as a nonassortative dilution of pteridophyte spores, allowing around 4% of the American species in each family to pass through.

In sum, distribution pattern analysis combined with island biogeographical concepts show that the pteridophyte flora of Galápagos is a diluted subset of the American pteridophyte flora, and that it is randomly distributed within the islands. Hence, it is in any aspect a perfectly harmonic flora. See Adsersen (1988) for a more extensive discussion.

Traits of the Distribution Pattern of the Entire Vascular Flora

A distribution pattern analysis based on updated records for the spermatophytes has not been made, and detailed information on the species pool for seed plants similar to that in Tryon & Tryon (1982) is not available, so we cannot yet respond to questions about seed plants with answers as thorough as those above. The same must be said for the entire vascular flora.

The vascular flora is the entity most often considered in biogeographical analyses, thus in island

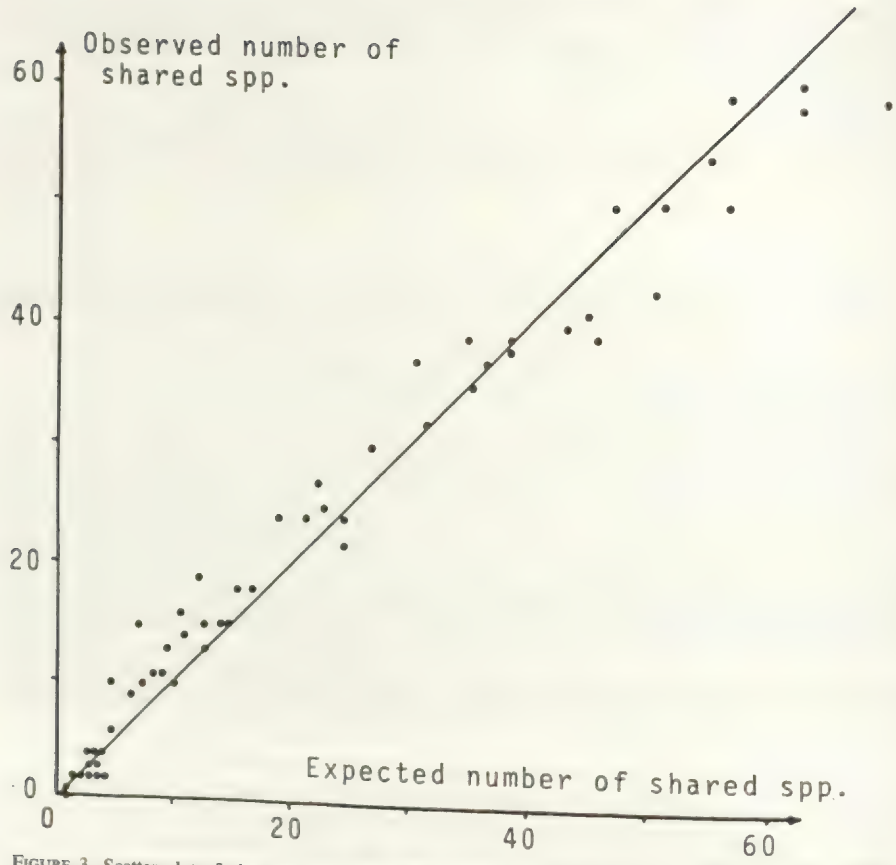

FIGURE 3. Scatter plot of observed number of pteridophytes shared by island pairs and expected number predicted by the calculus presented in Appendix I. The line is $y = x$, not a regression line.

biogeography. However, only van der Werff's (1983) treatment is without the biases inherent from the dot maps in Wiggins & Porter (1971). He found that the vascular flora is too heterogeneous for consideration, and by means of community data he distinguished "wet" and "dry" species. Subsequently he investigated the island species number in each of the two groups and concluded that habitat diversity offers the best explanation for the pattern. To divide the species into several ecologically defined groups and then study their distributions seems to be a good approach. On the other hand, his "wet" species include all the pteridophytes, so if, as suggested above, these differ in immigration pattern from the seed plants, his "wet" species may be an even more inconsistent group for island biogeography approaches than the entire vascular flora.

Already Robinson (1902) tried to reveal distribution patterns on the island flora level, based on common species numbers. His results rested on very few records, and Kroeber (1916), who had access to Stewart's material, had no difficulties in showing that Robinson's statements were spurious. Kroeber concluded that there were no surprising patterns in the distribution of plants in Galápagos, i.e., that neighbor islands had similar florula, and that the florula of large islands resembled those of other large islands more than those of small islands. Kroeber did not have the very good record representation, nor the similarity indices, nor the statistical concepts we have today. What he expected and found were deviations from random distributions of plants. He

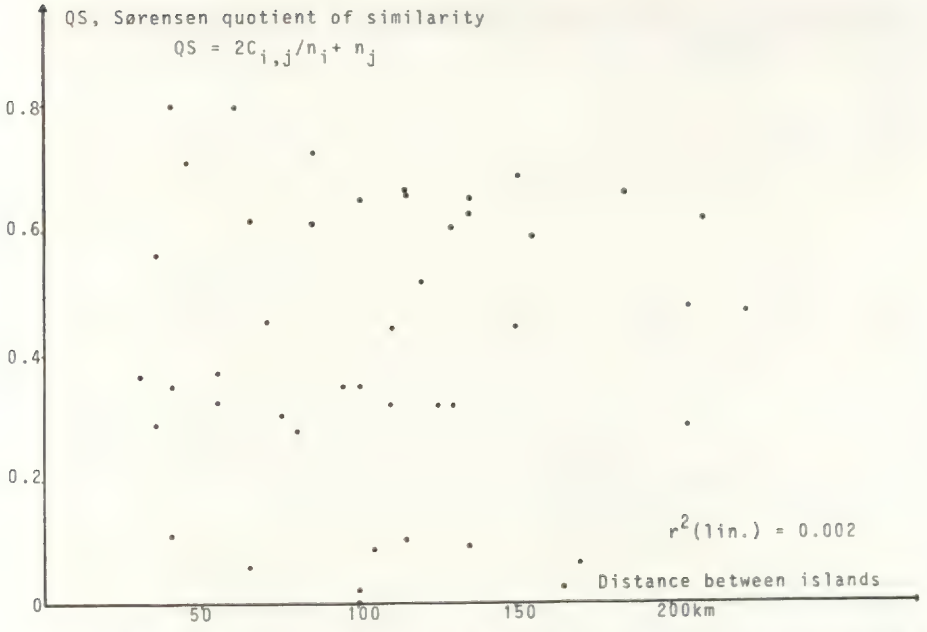

FIGURE 4. Scatter plot of interisland similarity of pteridophyte flora (expressed as Sørensen's index of similarity) and interisland distance.

emphasized that the western islands resemble each other more than they resemble the eastern islands with respect to floristic composition. There are reasons to believe that Kroeber was right; it is not difficult to make lists of eastern and western plants, as shown in Table 2. The plants included grow in different habitats, and each of the plants occurs on more than one island. The question is whether the lists comprise more or fewer species than should be expected from the general pattern, but first when the intra-archipelago pattern of distribution is known thoroughly, it will be possible to examine this, and thus establish whether the groups represented by the lists differ statistically significant in number from what should be expected. If, and only if, there are more eastern respectively western plants than should be expected, it has been shown by analysis on island flora level, that Galápagos is divided in an eastern and a western phytogeographical part. Other units may be defined too. Such units constitute far more objective material for studies of evolutionary, successional, immigrational, ecological, and vulcanological sequences and patterns than the more commonly presented *ad hoc* selected examples of strange plants and animals to illustrate island peculiarities.

At the community level of organization, distribution data are usually referred to phytosociological units and not to species. However, Hamann (1981), in his monograph on plant communities in Galápagos, added comments on the distribution of plants from a species-correlation view, based on community data, and he was able to indicate a number of correlations between plant species by means of a chi^2-analysis. This procedure tests the actual distribution against a random distribution of species within the communities. Deviations from this pattern are most often interpreted as due to different ecological requirements for the species, but differences in geographical ranges for the species in question will also give deviations. The analysis could be refined by setting up another null hypothesis in which the geographical distribution pattern is accounted for. In this way the patterns that belong to the ecological plant geography could be identified more clearly.

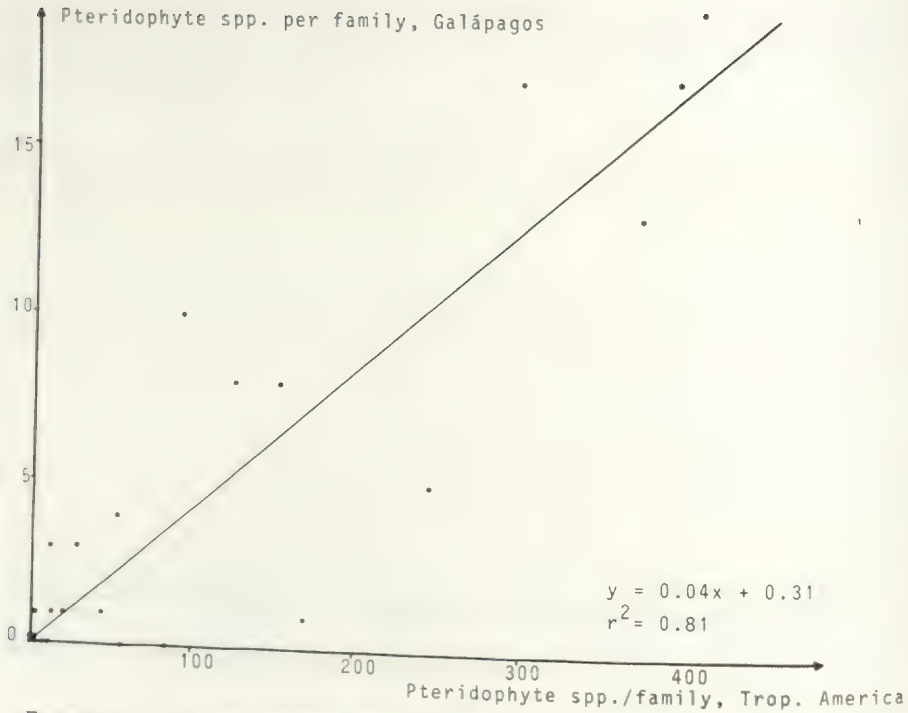

FIGURE 5. Correlation between species per family in Galápagos pteridophytes and in neotropical pteridophytes (the latter data, and family concept, from Tryon & Tryon, 1982). The Galápagos pteridophyte flora appears to be harmonic, and a 4% "dilution" of the neotropical one.

TABLE 2. Plants with eastern and western distributions in Galápagos. (For author names, see Wiggins & Porter, 1971.)

EASTERN PLANTS	WESTERN PLANTS
Acacia insulae-iacobi	*Baccharis gnidiifolia*
Cordia scouleri	*Calceolaria meistantha*
Cyperus elegans	*Castilleja arvensis*
Cyperus grandifolius	*Cordia revoluta*
Desmanthus virgatus	*Dodonea viscosa*
Eleocharis nodulosa	*Drymaria rotundifolia*
Encelia hispida	*Duranta dombeyana*
Grabowskia boerhaaviaefolia	*Duranta repens*
Lithophila radicata	*Froelichia juncea*
Ludwigia erecta	*Lippia rosmarinifolia*
Miconia robinsoniana	*Mollugo snodgrassii*
Neptunia plena	*Opuntia insularis*
Piscidia carthagenensis	*Pennisetum pauperum*
Prosopis juliflora	*Urocarpidium insulare*
Ruellia floribunda	

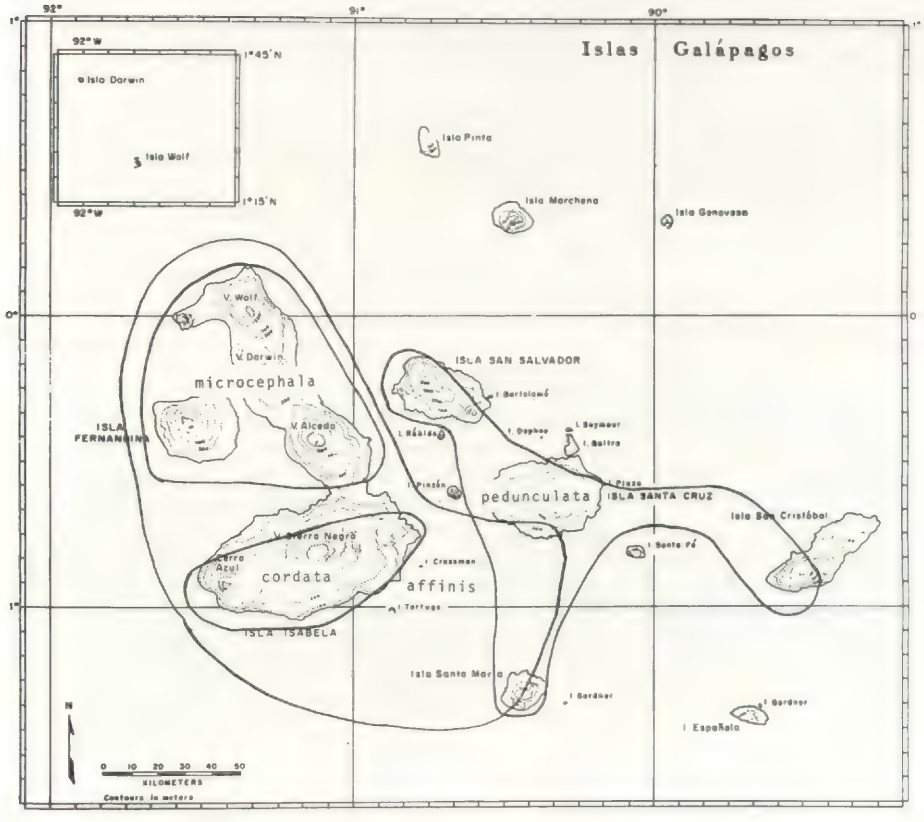

FIGURE 6. Distributions of the widespread *Scalesia* taxa. (Taxonomic concept as in Eliasson, 1974).

DISTRIBUTION PATTERNS AND EVOLUTIONARY TRAITS

As briefly mentioned above, evolution contributes significantly to species numbers in Galápagos, but this has been neglected in the examinations on the island flora level. However, there are reasons to believe that examinations on the distribution patterns of endemics would yield interesting results. Just to mention a few examples, among the most widespread and common ferns in Galápagos are the following endemics: *Polypodium tridens, P. insularis, Asplenium formosum* var. *carolinum,* and *Notholaena galapagensis*. These comprise 57% of the endemic pteridophytes, and these are among the ferns that extend farthest into the arid zones. The remaining three endemic pteridophytes are less common and are restricted to the humid zone, but still they are widespread. It has been stated that island endemics tend to have smaller dispersal capabilities than their ancestors (Carlquist, 1974); this obviously does not apply to the pteridophytes.

Species distribution patterns may elucidate problems on lower levels than that of entire island floras. For example, within genera where speciation is prominent, the distribution pattern may give hints on phylogeny. This may be illustrated by the three endemic asteraceous genera *Scalesia, Lecocarpus,* and *Darwiniothamnus,* which have quite different distribution patterns.

The distribution pattern of *Scalesia* taxa is complex, but it is worth noticing that sympatry among *Scalesia* species is exceptional (Figs. 6–7). Only *S. affinis* shows genuine sympatry with more than one species, and most species occur in small areas. The fact that almost all of the islands have

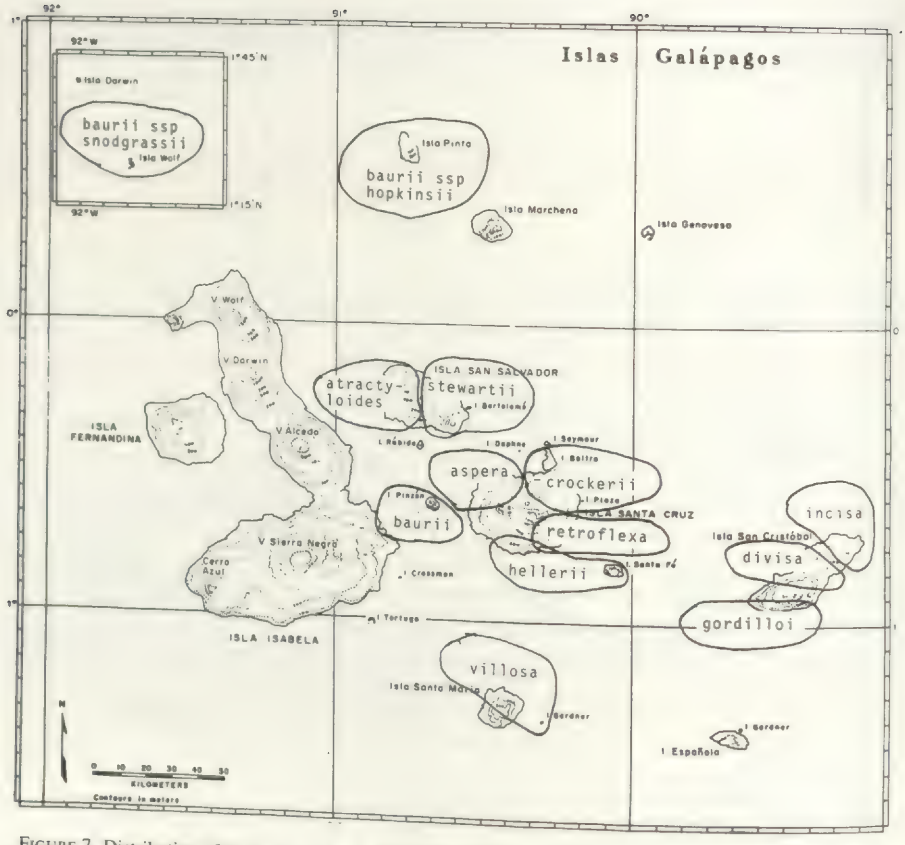

FIGURE 7. Distribution of *Scalesia* taxa with restricted ranges. (Taxonomic concept as in Eliasson, 1974, and Hamann & Wium-Andersen, 1986).

representatives of the genus proves that interisland dispersal has occurred, but the existence of the many taxa with small distribution areas indicates that successful dispersal is very infrequent. This leads to the conclusion that the widespread species probably are the most ancient ones. Eliasson (1974) considered *S. cordata* and *S. microcephala* primitive and *S. affinis* advanced. However, *S. affinis* has the typical distribution pattern of an "old" species. Analysis carried out on similarities of essential oil composition (Adsersen & Adsersen, in prep.) shows clearly that *S. cordata, S. affinis, S. microcephala,* and *S. pedunculata* form an entity, whereas the species with small distribution areas split into several chemically defined groups. Thus the distribution pattern suggests an alternative to postulating phylogeny of the genus based on morphology, and chemical data seem to give most support to the model suggested by distribution data.

Evolution within *Lecocarpus* is understandable in connection with present distributions. From *Acanthospermum microcarpum*, a herbaceous species still occurring in Floreana, a ligneous plant evolved with similar spiny pseudofruits. This spread to San Cristóbal, where it acquired diaspore variability (*L. darwinii*). The remaining stock on Floreana evolved leaf dissection, and dispersal took place to Española where reduction of ray floret number led to the present *L. lecocarpoides*. On Floreana, the pseudofruit developed a wing by fusion of the prickles, characteristic for *L. pinnatifidus* (Adsersen, 1980).

Darwiniothamnus is a genus with easily dispersed fruits. The distribution of *Darwiniothamnus* as

we conceive the genus (Lawesson & Adsersen, 1987) and the morphology of the three species show that *D. alternifolius* or something very similar immigrated to south Isabela. A line with condensed leaf whorls and inflorescences evolved (an adaptation to garua conditions?). This line dichotomized into a broad-leaved line, *D. lancifolius* (Hook.f.) Harling, which spread to the north, and a narrow-leaved line, *D. tenuifolius* (Hook.f.) Harling, which spread to the south and the east. Permanently the trade wind blows *D. tenuifolius* fruits into the *D. lancifolius* stands, so rather often *D. tenuifolius* or intermediates are found in the *D. lancifolius* stands—previously raising doubts of the integrity of *D. tenuifolius* and *D. lancifolius*. But, unlike *Scalesia*, the three species exhibit perfect sympatry on Sierra Negra. Hence the variation cannot be interpreted as habitat-induced, leaving no doubt that all three taxa are valid species.

Conclusions

The present natural flora and vegetation are results of events and processes in the past. Some events have been as dramatic as eruptions while others have been as subtle as the arrival of the propagule that became the origin of *Darwiniothamnus*. Some processes were as slow as the radiative evolution of *Scalesia*, or formation of soils; others were as rapid as the recovery of vegetation after superficial fires. In any case, the intra-archipelago distribution pattern of the vascular plants is probably the best evidence of these events and processes. If this evidence is recognized in its full extension, it becomes possible to evaluate the patterns statistically and to set up hypotheses on chronology for evolutionary, successional, chorological, and landscape-forming sequences.

The basic data, the species distribution records, are of obvious importance for monitoring and controlling aspects of the management of the Galápagos National Park. I anticipate that great part of what will be achieved by the scientific evaluation of intra-archipelago distributions will be applicable to management too, in the form of models of flora and vegetation development with predictive value.

Galápagos shows still, in spite of disturbances on the vegetation and habitat level, an almost complete picture of natural species distribution. This is a very good background when the effects of area use, introduction of alien animals and plants, fire, eruptions, and erosion must be evaluated and predicted in park management.

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APPENDIX I.

Calculation of null hypothesis of number of species common to two islands (coincidence number):

Let n_i be the number of species on island i, and let $C_{i,j}$ be the number of species that occur on both island i and island j.

Assume that the total number of coincidences between all pairs of islands, $\Sigma C_{i,j} = J$, is a characteristic constant of the given taxon in the given archipelago with N islands.

The null hypothesis is: that expected $C_{i,j}$ is proportional to n_i and to n_j, or $C_{i,j} = k\, n_i n_j$. J coincidences are now to be distributed proportionally among the $N(N-1)/2$ pairs of islands, according to the values of $k\, n_i n_j$. This infers that $k = J/\Sigma n_i n_j$ $(i > j)$.

Expected $C_{i,j}$ becomes $n_i n_j J/\Sigma n_i n_j$ $(i > j)$.

The accordance between the set of expected and the set of observed $C_{i,j}$ may be tested by a chi^2-test.

A paper on this calculation, its relation to other algorithms, and its application for setting up similarity matrices is under preparation.

FERNS AS INDICATORS OF VEGETATION TYPES IN THE GALAPAGOS ARCHIPELAGO[1]

Henk van der Werff[2]

ABSTRACT

The vegetation zones of Santa Cruz Island are briefly described and ferns present in these zones are listed. The most important environmental factor that determines the vegetation type is, on Santa Cruz, the amount of precipitation and presence or absence of a pronounced dry season. Because ferns are well represented in the Galápagos flora and have a narrow ecological range, they readily characterize the various vegetation types. Once the vegetation types on Santa Cruz are defined by their fern species, comparisons with vegetation types on other islands are possible, using fern species as ecological markers. Vegetation types of the Galápagos are also briefly compared with those of the mainland, and differences in vegetation structures on the Galápagos and the mainland are discussed.

From the earliest exploration onward, botanists and other scientists have been fascinated by the unusual, highly endemic flora of the Galápagos. More than a century of botanical exploration has resulted in the excellent *Flora of the Galápagos Islands* (Wiggins & Porter, 1971). Although species additional to the *Flora* are still being discovered (for bibliography up to 1980, see Schofield, 1980), the collecting phase of Galápagos botany is largely over. The *Flora*, however, makes studies of the Galápagos vegetation and species associations much easier because identification of the plants is no longer as time-consuming as it was (and still is for nearly all other neotropical areas). Wiggins & Porter (1971) included brief descriptions of the main plant communities, and more detailed descriptions were published a few years later (van der Werff, 1978; Hamann, 1981); these descriptions were based on structure and on floristic composition of the communities. These vegetation studies showed that there are profound differences in vegetation types among the islands; it also became clear that structurally similar vegetation types occurring on different islands do not necessarily occur under the same habitat conditions and that, for instance, evergreen scrub on Isabela is floristically quite different from evergreen scrub dominated by *Miconia robinsoniana* on Santa Cruz. In this contribution, the vegetation zonation found on Santa Cruz, which is both the most complex and best known in the archipelago, is briefly described, and the main vegetation types are defined with the help of ferns present. In this way, ferns make a comparison between vegetation types on different islands possible and even can be used to make some very general remarks on relationships between the Galápagos and continental neotropical vegetation types.

The nomenclature of the Galápagos ferns follows Wiggins & Porter (1971), with one exception. Several segregate genera, mostly of *Polypodium* and *Lycopodium*, are now more or less widely accepted, and the concepts of *Cheilanthes* and *Notholaena* have also changed (Tryon & Tryon, 1982), but I use the names from Wiggins & Porter (1971) here. The only exception is that I accept *Thelypteris oligocarpa* (Humb. & Bonpl. ex Willd.) Ching as the correct name for the specimens identified as *Thelypteris pilosula* (van der Werff, 1977). Bringing the names of the Galápagos ferns up to date is outside the scope of this contribution.

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Climate

In many books (Carlquist, 1974, may have been a source) and documentaries, the Galápagos Islands are described or depicted as xeric or desert islands. While most of the island area is indeed xeric, there are also areas with a definitely mesic climate. Variation in climate can be abrupt over small distances and is correlated with equally abrupt changes in vegetation.

There are two seasons in the Galápagos archipelago, a warm one from January to June, and a cool one from June to January. During the warm season skies are generally clear, and, as a result of heating by the sun, large cumulus clouds can be formed, which result in local, heavy showers. These showers are fairly evenly distributed over the archipelago, although the interiors of the large islands tend to receive more rain. Winds are not strong during the warm season and may blow from any direction—there is no trade wind.

There is a steady southeastern trade wind during the cool season, which pushes moisture-saturated air against the islands. This air is forced uphill on the windward slopes of the higher islands, which results in condensation, fog, or light rains. The intensity of this phenomenon, called *garúa*, depends on steepness of slope and exposure to trade winds. The effect of *garúa* is slight at low elevations and becomes more intense with increasing elevation, up to about 1,000–1,300 m. At this elevation occurs an inversion layer, which prevents the moist air from rising any further. The summit areas of the highest volcanoes (on Isabela and Fernandina) do not receive moisture from the *garúa* and dry out completely during the cool season, just as the coastal areas do.

Because the *garúa* is a consequence of moist air forced up on the windward slopes of the islands, its effect is strongest on the windward slopes and very weak on the leeward slopes. On Santa Cruz, for instance, the only moisture the leeward slopes receive is *garúa* blown over and around the summit area, which descends at most a few hundred meters. This explains why vegetation types can have widely different altitudinal ranges on the windward and leeward slopes. The same applies to species distribution; the fact that *Bursera graveolens* is common at 450 m on the northern (leeward) slope of Santa Cruz gives no information whatsoever about the altitudinal distribution of that species on the southern (windward) slope, where it does not occur above 100 m.

It is also important to keep in mind the tremendous variation in rainfall from year to year. This variation is not so great in the cool, *garúa* season; the *garúa*, in form of fog or light rain, is nearly always there, although there is variation in intensity. What does vary, however, are the rains during the warm season. Excessively wet seasons, which occur once or twice a decade and are called *El Niño*, can increase rainfall a hundredfold over that of dry years. For example, during April–May 1982, the Charles Darwin Research Station received 8.5 mm of rain; during the same period in 1983 the rainfall was 1,094.4 mm (CDRS Annual Report, 1983).

Main Vegetation Types on Santa Cruz Island

In this section the known distribution and structure of the species associations and their common fern species on Santa Cruz are briefly described. For more detailed descriptions, see van der Werff (1978) and Hamann (1981). The coastal vegetation, forming a narrow belt along the shoreline, is not included because no ferns have been reported from it.

The distribution of the most common fern species on Santa Cruz is presented in Table 1, which is based on 116, 10 × 40-m quadrats. The quadrats were not placed at random, but in stands, homogeneous in vegetation structure and substrate, of the various vegetation types. The recognition and naming of the species associations and their hierarchical classification follows the methodology of Braun-Blanquet (1964).

TABLE 1. Distribution of representative fern species over the main species associations on Santa Cruz. Heading columns, the numbers for species associations, correspond with those used in the text. The numbers in the columns refer to the frequency of the species: 5 indicates the presence in 80–100% of the quadrats made in that vegetation type, 4 = 60–80%, 3 = 40–60%, 2 = 20–40%, 1 < 20%, and + very rarely found in that vegetation type. Usually, a high frequency coincides with abundance, that is, the number of individual plants in a quadrat is high, but this is not necessarily so.

	IIa1	IIa2	IIa3	IIb1	IIb2	IIc	IId
Doryopteris pedata	5	5	5	5	4	4	5
Asplenium auritum	4	5	5	5	5	4	2
Asplenium formosum	3	5	4	5	4	+	2
Polypodium lanceolatum	3	4	3	5	5	1	
Polypodium aureum	+		1	2	2	3	+
Polypodium tridens	2	1	+			+	4
Asplenium praemorsum	2			5	5	3	3
Ctenitis sloanei		2	+	5	5	4	
Thelypteris tetragona	2	4	3	4	1		
Polypodium steirolepis	3		1	5	5		
Polypodium phyllitidis		4	+	5	4		
Adiantum henslovianum		3	3	5	+		
Polypodium dispersum	5	5	4				
Polypodium insularum	4	4	1				
Hemionitis palmata	1	5	1				
Trachypteris pinnata	4	+	2				
Asplenium pumilum	2	4	2	1			
Nephrolepis cordifolia				3	5	4	2
Blechnum occidentale				4	5	2	4
Thelypteris oligocarpa				3	3	5	5
Pteridium aquilinum				+	2	5	5
Lycopodium passerinoides	1			2	4	3	+
Ctenitis pleiosorus				3	5	4	
Trichomanes reptans				2	5	2	
Asplenium feei				2	5	4	
Asplenium cristatum				5	5	2	
Pteris quadriaurita				4	5	+	
Thelypteris patens				2	3	2	
Dennstaedtia globulifera				2	5	2	
Thelypteris poiteana				1	3		
Polypodium angustifolium				1	5		
Adiantum macrophyllum				1	2		
Antrophyum lineatum				+	3		
Lycopodium setaceum				+	3		
Diplazium subobtusum					3	3	
Thelypteris balbisii					+	1	
Blechnum polypodioides						5	4
Pityrogramma calomelanos var. *calomelanos*						3	5
Asplenium serra						4	1
Lycopodium clavatum						4	1
Hypolepis hostilis						4	
Cyathea weatherbyana						4	
Tectaria aequatoriensis						2	
Elaphoglossum firmum						2	
Lycopodium cernuum						2	
Dicranopteris flexuosa						1	
Elaphoglossum minutum						1	
Thelypteris linkiana						1	
Histiopteris incisa						1	
Ophioglossum reticulatum							3
Mildella intramarginalis							2
Pityrogramma tartarea							+

I. ALLIANCE BURSERION GRAVEOLENTIS

The species associations on Santa Cruz fell into two alliances, of which the Burserion graveolentis agrees with the arid zone of earlier authors. It is found in areas with a pronounced dry season (June–January). The growing period for the vegetation is during the warm season, January–May. On Santa Cruz it occurs on the southern slope from sea level to about 70 m elevation, and on the northern slope from sea level to about 490 m. Within this alliance, two associations, occurring on different substrates, can be recognized on Santa Cruz.

Ia. ABUTILETUM DEPAUPERATI

Structure. A dry-season deciduous forest dominated by *Bursera graveolens* and *Piscidia carthagenensis.*

Distribution. On southern Santa Cruz from sea level to about 70 m, on northern Santa Cruz from 60 to about 500 m, and on the eastern slope from sea level to about 150 m.

Ferns present. Ferns are occasionally found in this association, but are rare. All belong to species more commonly found in other vegetation types and none are characteristic for this vegetation type. Species found are *Adiantum concinnum, Trachypteris pinnata,* and (once) *Polypodium tridens.*

Ib. CYPERETUM ELEGANTIS

Structure. A sparse, shrubby vegetation with an open herb layer. It occurs in areas with a prolonged dry season and only on red, clayey soils, where it replaces the dry-season deciduous forest found on lava.

Distribution. The northeastern part of Santa Cruz, from the Bolivar channel to the coast opposite Plaza Island, from sea level to about 60 m.

Ferns present. Ferns have not been found in this vegetation type.

II. ALLIANCE PSYCHOTRION RUFIPEDIS

The second of the two alliances recognized on Santa Cruz includes all other species associations. It occurs in areas where the main source of moisture for the vegetation is not the rains during the warm season, but the *garúa* during the cool season and thus the growing period for the vegetation is during the cool season from June to January, while there may be a resting period during the warm season.

The vegetation types included in this alliance show great variation in structure, ranging from herbaceous vegetation to forest, but all are evergreen or semideciduous. Ferns are common in these habitats, several species are good indicators for one or two species associations, but a few are common in all species associations of this alliance. These ecologically nonspecialized ferns include *Asplenium auritum, A. formosum, A. praemorsum, Doryopteris pedata, Polypodium lanceolatum,* and the less common *Polypodium aureum.*

IIa. PSIDIO-ANREDERETUM RAMOSAE

Structure. A more or less closed, semideciduous or evergreen forest.

Distribution. On the southern slope of Santa Cruz, from 70 to 200 m (where the cultivated zone starts; between 200 and 490 m the natural vegetation has been removed and the 200 m limit is not

natural), on the eastern slope from 200 to 420 m, and on the northern slope from about 500 to 600 m.
Ferns present. Common ferns restricted to this association are *Polypodium dispersum, P. insularum, Asplenium pumilum* (occurs rarely in the wetter *Scalesia* forest; has a strong preference for unweathered lava blocks), and to a lesser degree *Hemionitis palmata* and *Trachypteris pinnata.* The last two species show an optimum presence in one of the three subassociations (see below) and have an uneven distribution in this association.

IIa1. PISCIDIO-TRACHYPTERIDETOSUM

Structure. A semideciduous forest, dominated by *Piscidia carthagenensis, Pisonia floribunda,* and *Psidium galapageium.*
Distribution. On the southern slope of Santa Cruz, from 70 to 150 m, on the eastern slope from 200 to 240 m, and on the northern slope from about 500 to 600 m.
Ferns present. Trachypteris pinnata is a good indicator for this subassociation. Although it also occurs sparingly outside this vegetation type, it reaches its greatest frequency and abundance here. A characteristic, but uncommon, species is *Polypodium polypodioides,* a rather inconspicuous epiphyte.
Note. This vegetation type corresponds with the transition zone vegetation of Wiggins & Porter (1971). Structurally, it is an intermediate between the (drier) dry-season deciduous forest and the (wetter) evergreen forest dominated by *Scalesia pedunculata.* Floristically, however, it is much more similar to the evergreen than the deciduous forests. Hence, in the floristic classification it is included in the *Psychotrion rufipedis* alliance.

IIa2. SCALESIO-HEMIONITIDETOSUM

Structure. A closed evergreen forest dominated by *Scalesia pedunculata.*
Distribution. On the southern slope of Santa Cruz, from 150 to 200 m.
Ferns present. A common species in this subassociation, but rare outside it, is *Hemionitis palmata.*
Note. Based on their floristic composition, the disjunct remnants of the *Scalesia pedunculata* forests are divided into three subassociations. The two drier ones, the scalesia-hemionitidetosum and the darwiniothamno-rhynchosietosum, differ in that the latter occurs in an area with fewer surface rocks and has a more open canopy layer, where a number of species from the drier semideciduous forest (such as *Trachypteris pinnata*) are present. The third type of *Scalesia pedunculata* forest occurs under wetter conditions than the other two. Two terrestrial ferns (*Adiantum henslovianum* and *Thelypteris tetragona*) are common in all three types of *Scalesia pedunculata* forest and are uncommon or lacking outside it.

IIa3. DARWINIOTHAMNO-RHYNCHOSIETOSUM

Structure. A more or less closed evergreen forest, dominated by *Scalesia pedunculata.*
Distribution. On the eastern slope of Santa Cruz, from 240 to 420 m.
Ferns present. Although ferns are rather common in this vegetation type, none are restricted to or indicative for it.

IIb. ACNISTO-URERETUM CARACASANAE

Structure. A closed or open evergreen forest.
Distribution. The known distribution probably does not reflect the original distribution, because no

undisturbed vegetation was found on the southern slope of Santa Cruz in areas where this association was thought to occur. Hence it is only known from areas on the eastern (450–550 m) and northern (600–740 m) slopes.

Ferns present. The wetter conditions under which this association is found are reflected in the disappearance of the indicator species of the Psidio-Anrederetum ramosae and its three subassociations, the increased frequency of such species as *Ctenitis sloanei*, *Asplenium praemorsum*, *Polypodium steirolepis*, and *Lycopodium passerinoides* and the presence of a number of species not found in drier areas. Of these additional species, *Adiantum macrophyllum*, *Antrophyum lineatum*, *Lycopodium setaceum*, *Polypodium angustifolium*, *Pteris quadriaurita*, and *Thelypteris poiteana* seem restricted to this association, while *Asplenium feei*, *A. cristatum*, *Blechnum occidentale*, *Ctenitis pleiosorus*, *Dennstaedtia globulifera*, *Nephrolepis cordifolia*, *Pteridium aquilinum*, *Thelypteris oligocarpa*, *T. patens*, and *Trichomanes reptans* also occur in other associations.

IIb1. SCALESIO-GALIETOSUM

Structure. A closed evergreen forest dominated by *Scalesia pedunculata*.

Distribution. On the eastern slope of Santa Cruz, from 450 to 550 m, on the northern slope from 600 to 740 m.

Ferns present. This subassociation does not have indicator species among the ferns, but it is characterized by the presence of such relatively drought-resistant species as *Adiantum henslovianum* and *Thelypteris tetragona* and of more such moisture-requiring species as *Ctenitis pleiosorus*, *Blechnum occidentale*, *Asplenium cristatum*, and *Pteris quadriaurita*.

IIb2. TOURNEFORTIO-ANTROPHYETOSUM

Structure. An open evergreen forest very rich in epiphytes.

Distribution. Only known from a small area on the upper northern slope of Santa Cruz. Although it currently covers only a small area, this subassociation is included among the main vegetation types for two reasons. First, earlier workers (for instance, Bowman, 1961) described this subassociation (as the Brown Zone) as one of the main vegetation zones on the southern slope of Santa Cruz. Second, it represents both structurally and floristically a transition from the evergreen *Scalesia* forest to the evergreen *Miconia* shrub. Human disturbance has greatly reduced the area covered with this vegetation type and it is in danger of disappearing altogether unless conservation measures are taken.

Ferns present. The following ferns have their optimum in this vegetation type: *Antrophyum lineatum*, *Dennstaedtia globulifera*, *Lycopodium setaceum*, *Polypodium angustifolium*, and *Trichomanes reptans*. *Diplazium subobtusum* is restricted to this and the following vegetation type.

Note. The name Brown Zone has been given to this vegetation type because of the presence of large, conspicuous masses of epiphytic *Frullania* (Hepaticae) species. This name is a misnomer because *Frullania* species (Gradstein & Weber, 1982, list 14 *Frullania* species from the Galápagos), not only occur in other vegetation types, but can form similar large, brown, epiphytic masses in the Transition Zone (piscidio-trachypteridetosum). Thus in the vegetation types bordering the *Scalesia* forests, both in the drier forests at lower elevation and wetter forests at higher elevation, large masses of epiphytic *Frullania* species occur, but not in the *Scalesia* forests. The most likely explanation for the lack of large masses of small (and large) epiphytes is that *Scalesia pedunculata* has the characteristics of secondary forest trees, such as rapid growth, soft wood, and short life span (van der Werff, 1978; Hamann, 1979a). The soft wood and short life span make the growth of large masses of epiphytes, such as *Frullania* spp., or of large epiphytes, such as *Polypodium aureum* and *Tillandsia insularis*, on *Scalesia* trees almost impossible. The distribution of epiphytes on Santa

Cruz is thus strongly influenced by the distribution of the few species of slow-growing tree species with hard wood (such as *Psidium galapageium, Zanthoxylum fagara,* and *Piscidia carthagenensis*), which serve as hosts. The lack of suitable support trees can also explain the absence of large lianas and scandent hemiepiphytes such as *Polybotrya* from the Galápagos Islands.

IIc. MICONIETUM ROBINSONIANAE

Structure. A closed evergreen scrub, dominated by *Miconia robinsoniana.*
Distribution. The southern slope of Santa Cruz from 500 to 570 m. Conversion of native vegetation to pastureland and possibly also the occurrence of large fires have greatly reduced the area covered with *Miconia* scrub.
Ferns present. As can be expected when vegetation changes from forest to scrub, the number of epiphytes diminishes drastically. In the tournefortio-antrophyetosum, 16 epiphytic species are found, in the *Miconia* scrub only five. On the other hand, the *Miconia* scrub harbors several fern species not found in other vegetation types, such as *Cyathea weatherbyana* (which occasionally forms dense stands), *Hypolepis hostilis,* and *Tectaria aequatoriensis. Blechnum polypodioides* is very common in this and the following vegetation type, *Asplenium serra* less so. A few rare ferns are restricted to wet clay banks along streams through the *Miconia* scrub, but have not been found away from streams: *Asplenium otites, Blechnum lehmannii,* and *Thelypteris linkiana. Arachniodes denticulata* and *Thelypteris gardneriana* are found in similar habitats on San Cristóbal. Several ferns are common in disturbed areas (sunny streambanks, trail sides, etc.), but are rare or lacking inside the *Miconia* scrub. These include *Dicranopteris flexuosa, Elaphoglossum firmum, E. minutum,* and *Lycopodium cernuum.*

IId. HABENARIO-TRISETETUM HOWELLII

Structure. An evergreen, herbaceous vegetation without dominating species.
Distribution. In the wind-exposed summit area of Santa Cruz above 530 m. In wind-protected places (such as on the north slope), a forest or scrub vegetation may extend up to 750 m.
Note. Although this vegetation type is reasonably homogeneous on Santa Cruz (see Itow, this symposium, for a discussion of the several divisions within this vegetation type), the structural vegetation type (called "pampa" vegetation), occurs also on other islands, sometimes with quite different species associations, which grow under different moisture regimes. The lack of woody vegetation in the pampa zone greatly reduces the leaf surface available for condensation of the *garúa* and thus reduces the amount of moisture available to the plants. The driest type of pampa vegetation on the southern slope of Santa Cruz is characterized by ferns that can tolerate some dryness, such as *Pityrogramma calomelanos, Mildella intramarginalis, Polypodium tridens,* and *Pteridium aquilinum.* With increasing elevation and/or steepness of slope the effect of *garúa* becomes stronger; many of the native Galápagos phanerogam species cannot grow under such wet conditions with the result that under the wettest conditions on Santa Cruz the vegetation consists of *Sphagnum* bogs with scattered tree ferns and some *Blechnum falciforme* and *Elaphoglossum glossophyllum.* Itow (this symposium) describes these vegetation types in detail.

On Cerro Azul (Isabela Island) similar wet pampa areas occur. Common ferns in the drier pampa areas on Cerro Azul are *Mildella intramarginalis* and *Pteridium aquilinum.* In the wettest areas terrestrial mosses (*Breutelia tomentosa, Thuidium recognitum*) dominate and pteridophytes are common, with *Cyathea weatherbyana, Blechnum falciforme, Elaphoglossum glossophyllum, Equisetum bogotense, Rumohra adiantiformis, Thelypteris cheilanthoides, T. pavoniana, T. oligocarpa, T. thomsonii, Dryopteris wallichiana* (the oldest name for the species called *D. parallelogramma* in van der Werff, 1977), and *Hymenophyllum plumieri* present. These habitats, where

TABLE 2. The Sorensen indices of similarity ($I_s = 2C/A+B \times 100$) between the species associations on Santa Cruz. Numbers for species associations correspond with those used in the text.

	Ia	IIa1	IIa2	IIa3	IIb1	IIb2	IIc	IId
Ia	—							
IIa1	41	—						
IIa2	27	73	—					
IIa3	26	66	66	—				
IIb1	16	54	59	60	—			
IIb2	8	42	39	38	74	—		
IIc	6	26	27	26	45	47	—	
IId	4	24	25	30	37	30	41	—

native flowering plants are largely replaced by bryophytes and pteridophytes, are the wettest I have seen on the Galápagos Islands.

ADDITIONAL HABITATS

An additional vegetation type restricted to Isabela and Fernandina are the dry summits of the volcanoes above the inversion layer. The climate in these areas is much like the coastal zones; rainfall is sporadic during the warm season and there is very little precipitation during the cool season. Characteristic ferns here are *Cheilanthes myriophylla*, *Notholaena aurea*, and *Pellaea sagittata*.

Fumarole activity has been reported from several of the Galápagos Islands. Galápagos fumaroles are rarely large and powerful (as for example, the "geyser" on Alcedo), and here the vegetation is restricted to a few species (*Cyperus ligularis* and *Scoparia dulcis*). In most fumarole areas one finds small vents, which emit moist, warm air. A few fern species are frequently found around these vents and include *Pityrogramma calomelanos* var. *aureoflava* (almost never var. *calomelanos*), *Dicranopteris flexuosa*, *Lycopodium cernuum*, *Nephrolepis biserrata*, and sometimes *Psilotum nudum*.

RECONSTRUCTION OF VEGETATION ZONATION

The sequence of vegetation types occurring from the coast to the summit of Santa Cruz, as described above, is an abstraction and does not exist anymore. This is mainly because large parts of the windward slope, where the mesic types were optimally developed, have been brought into cultivation and the natural vegetation has been removed. There are several reasons why the vegetation zonation can be reconstructed with confidence. First, the proposed sequence of the vegetation structure is correlated with changes in climate, and there are no abrupt changes in vegetation structure between adjacent vegetation types. Going inland, one finds a change from deciduous to semideciduous to evergreen forest corresponding with an increase in rainfall and a more even distribution of the rainfall over the year. Further increases in rainfall lead to a gradual decrease of vegetation structure, from a closed evergreen forest, to open evergreen forest, to evergreen scrub, and finally to evergreen herbaceous vegetation. Comparable changes in vegetation structure corresponding with climatic changes have been reported from many other tropical areas and were extensively discussed by Beard (1955). A second argument rests upon the floristic similarities between the species associations found in Santa Cruz (Table 2). The formula for the Sorensen index of similarity between two species associations is $I_s = 2C/A+B \times 100$, where C represents the number of shared species between A and B, while A and B stand for the total number of species in associations A and B. In this calculation incidental species have been deleted; that is, a species

found only once in a given association is not counted. The indices indicate the same relationships between the vegetation types as the sequence based on the structure of the vegetation, and I therefore accept this as the original sequence of vegetation types found on Santa Cruz.

Size of the fern plants is correlated with increasing moisture and a more even distribution of moisture over the year. Ferns in the semideciduous forest and the driest types of evergreen forest are rather small; examples are *Trachypteris pinnata*, *Asplenium pumilum*, and *Polypodium dispersum*. Under slightly more mesic conditions, taller ferns occur, as *Thelypteris tetragona*, *Polypodium phyllitidis*, and *Adiantum henslovianum*. Common ferns in the open evergreen forest are *Dennstaedtia globulifera*, *Ctenitis pleiosorus*, and *Diplazium subobtusum*. In the *Miconia* scrub these same ferns plus *Pteridium aquilinum* and *Cyathea weatherbyana* are frequent; they are not part of the understory, but their fronds become part of shrub canopy, and their size depends on the size of the shrubs. With the absence of trees and shrubs in the pampa zone, all tall ferns, with the exception of *Pteridium aquilinum* and some stunted specimens of *Cyathea weatherbyana* in *Sphagnum* bogs, disappear. Low ferns such as *Doryopteris pedata*, *Blechnum polypodioides*, *Polypodium tridens*, and the slightly taller *Pityrogramma calomelanos* and *Thelypteris oligocarpa* (here smaller than in the wind-sheltered scrub or forest) dominate. Small ferns are, of course, also present in the *Miconia* scrub and the mesic forest types; the increase in size with more humidity applies only to the largest kinds of ferns in each community.

Because the effects of the *garúa* are strongest on the windward slope and the original mesic vegetation types were best developed there, it is highly desirable, both from conservation and scientific points of view, to protect a sufficiently wide strip of land along the windward slopes of Santa Cruz and San Cristóbal and to let the vegetation regenerate in this zone. Observations on vegetation recovery on Pinta (Hamann, 1979b) suggest strongly that a recovery of the native vegetation is likely, and it would be very valuable to have the most complex sequence of vegetation types known in the Galápagos Islands preserved.

Comparison with Other Islands

The vegetation types and species associations found on Santa Cruz Island are not representative for other islands (for detailed descriptions, see van der Werff, 1978, and Hamann, 1981). Two main factors are responsible for the differences in vegetation types among the islands. First, there can be variation in substrate; Santa Cruz is an older island where weathering of the lava has produced a definite soil layer in the mesic interior, while on younger islands, such as Isabela (Volcano Wolf), even under mesic conditions, there is virtually no soil present; the lava or cinders are only covered by a layer of humus and a forest is lacking. On Alcedo, large areas are covered by thick pumice deposits; the vegetation found there is floristically and structurally different from vegetation types on Santa Cruz. The second factor is floristic differences: Santa Cruz is the only island where *Scalesia pedunculata* forms extensive forest. On other islands different *Scalesia* species can dominate the vegetation, but these stands can be completely different in structure and floristic composition from the *Scalesia pedunculata* forests. Although this species also occurs on San Cristóbal and Sal Salvador, it does not form forests, probably due to destruction of the vegetation by activity of humans or introduced animals. Eliasson (1974) reported *Scalesia pedunculata* forests from Floreana; the presence of *Lippia* and *Macraea* in those forests strongly suggests that they occur under drier conditions than the *Scalesia pedunculata* forests on Santa Cruz. *Scalesia pedunculata* is not present on other islands; here forest is lacking in habitats where on Santa Cruz, *Scalesia* forests are found. For example, on Cerro Azul (Isabela) all vegetation types wetter than the semideciduous forest are evergreen herbaceous, without scrub or forest; on the windward slope of Alcedo, the semideciduous forest is followed by an extensive zone of scrub, dominated by *Psychotria rufipes* and *Tournefortia rufosericea*. The ferns in this scrub indicate that it corresponds with the *Scalesia* forests on Santa Cruz. Present throughout are *Ctenitis sloanei*, *Blechnum occidentale*, and *Pteris*

quadriaurita; more common in the lower (drier) part are *Polypodium phyllitidis, Adiantum henslovianum,* and *Polypodium dispersum,* while in the wettest scrub *Dennstaedtia cicutaria* (which largely replaces *D. globulifera* in the scrub) and *Thelypteris grandis* are very common, with *Pteridium aquilinum* and *Thelypteris oligocarpa* more common than in the drier parts and *Ctenitis pleiosorus* also present. Above this scrub zone is a zone with open evergreen forest very similar to the same vegetation type on Santa Cruz, with such species as *Hymenophyllum polyanthos, Polypodium angustifolium, Asplenium feei, A. serra, Ctenitis pleiosorus,* and *Dennstaedtia globulifera,* which is more common in forest habitat than *D. cicutaria.* With the exception of a few small tree fern brakes, an evergreen scrub comparable to the *Miconia* scrub and an evergreen herbaceous vegetation are lacking on Alcedo. The arborescent *Scalesia microcephala* occurs on Alcedo; it is present in the open evergreen forest and is the dominant species in large areas covered with shrubby savanna. Although dominated by a woody *Scalesia* species, this savanna is floristically very unlike the *Scalesia pedunculata* forest on Santa Cruz; and it occurs under climatic conditions similar to those found in the semideciduous forest on Santa Cruz.

Another vegetation type not present on Santa Cruz is the evergreen scrub found on a cinder substrate on several volcanoes on Isabela; it is well developed on Volcano Darwin. This scrub community is rather open; most species have small, coriaceous leaves; and it is rich (for the Galápagos) in species. Characteristic elements are *Linum harlingii, Dodonaea viscosa, Cordia* spp., *Darwiniothamnus, Tournefortia pubescens, Macraea laricifolia,* and *Lippia rosmarinifolia,* as well as *Opuntia* and *Jasminocereus.* Although this community has been compared to the evergreen *Miconia* scrub (Wiggins & Porter, 1971), it is floristically very different. Ferns are not common, but *Trachypteris pinnata, Cheilanthes microphylla,* and *Polypodium tridens* were present; these ferns indicate a moisture regime comparable to that in the semideciduous forest.

The available information shows that Santa Cruz has the most complex vegetation types. Mesic forests are lacking on Isabela and Fernandina, or, on Volcano Sierra Negra, are greatly disturbed; on Santiago introduced animals, particularly goats, have destroyed much of the vegetation; Floreana is a rather dry island (ferns characteristic for the open evergreen forest, evergreen scrub, and evergreen herbaceous vegetation are rare or lacking), and finally, San Cristóbal is also severely disturbed. This last island has a very wet summit and probably had a similar vegetation zonation to that of Santa Cruz.

The fact that structurally different vegetation types occur under similar climatic conditions on different islands complicates comparisons. However, ferns can be accurate indicators of habitats. More than a hundred species have been recorded from the archipelago; they are often common, easily identified, and many of the species have a narrow ecological range. By knowing the fern flora from a given locality, one can, with the help of Table 1, find out where its vegetation would fit in the vegetation sequence on Santa Cruz. Thus ferns can be used as a yardstick for comparison of vegetation types on different islands.

Comparison with the Mainland

Ferns also facilitate comparisons among vegetation types on the Galápagos Islands and the American continent. As can be expected, continental neotropical and Galápagos vegetation types show great differences in structure and floristic composition. A striking difference is the small number of tree species in the Galápagos archipelago. Santa Cruz, with an area of 904 km^2, has only 27 tree species, including "marginal" tree species as *Jasminocereus* and *Opuntia,* and five species restricted to the litoral zone (Table 3). On the other hand, three Ecuadorian mainland sites, Río Palenque (wet forest), Jauneche (moist forest), and Capeira (dry forest), with areas of respectively 1.0 km^2, 1.3 km^2, and 5 km^2, contained 154, 108, and 69 tree species with >10 cm DBH (Gentry & Dodson, 1987). The other strata in the Galápagos vegetation are similarly poor in species when compared with these continental sites. Given the importance of trees as elements determining the

TABLE 3. Indigenous trees on Santa Cruz. Code for distribution: A = neotropical; C = dry and/or coastal W South America; E = endemic; P = pantropical. When a species occurs in more than one vegetation type and has an optimum, its optimum is indicated by + +. I = Littoral Zone; II = Deciduous Forest; III = Semideciduous Forest; IV = Evergreen forest; V = Open Evergreen Forest.

	I	II	III	IV	V	Distr.	
Avicennia germinans	+					A	
Conocarpus erecta	+					A	
Hibiscus tiliaceus	+					P	
Laguncularia racemosa	+					A	
Rhizophora mangle	+					A	
Maytenus octogona	+	+				C	
Prospis juliflora	+	+				A	
Hippomane mancinella	+	+	+	+		A	
Acacia insulae-iacobi		+				A	
A. macracantha		+				A	
Jasminocereus thouarsii		+				E	
Bursera graveolens		+				A	
Cordia lutea	+	+				C	
Opuntia echios var. *gigantea*		+				E	
Parkinsonia aculeata		+				A	
Croton scouleri		+ +	+			E	
Erythrina velutina		+ +	+			A	
Piscidia carthagenensis		+	+			A	
Pisonia floribunda		+	+ +	+		E	
Psidium galapageium		+	+	+	+	E	
Scalesia pedunculata			+	+ +	+	E	
Trema micrantha			+	+		A	
Solanum erianthum				+		A	
Sapindus saponaria				+		A	
Acnistus ellipticus				+	+	E	
Tournefortia pubescens					+	E	
Zanthoxylum fagara					+	A	
	8	15	8	8	5	27	Total
	0	27	50	50	80	30	% Endemics

structure of the vegetation, it is not surprising that the vegetation types on the Galápagos are structurally less complex than those found on the mainland. Especially the wetter forests on Santa Cruz are much lower than forests under similar conditions on the American continent. These differences are summarized in Table 4, in which physiognomical names, names used in the *Flora of the Galápagos Islands* (Wiggins & Porter, 1971), corresponding species associations listed in this paper, and a brief characterization of the main vegetation types on Santa Cruz are presented together with the vegetation types predicted in the Holdridge system (Holdridge et al., 1971).

In this system, it is assumed that the undisturbed vegetation in a given area is largely determined by the climate and that, when climatic data are available, one can accurately predict the structure of the vegetation. This system has been widely used in the tropics and seems to work reasonably well. In the fourth column of Table 4, the predictions for the undisturbed vegetation based on climatic data applied to the Holdridge system are presented. These predictions are, in some cases, widely different from the actual vegetation; for example, the Holdridge system predicts a premontane moist or wet forest where an evergreen herbaceous vegetation is found. Unfavorable edaphic or climatic conditions are not likely to offer an explanation for the lack of forest on the upper slopes of Santa Cruz, as can be seen from the difficulties of keeping such introduced trees as *Cinchona succirubra* under control.

TABLE 4. Summary of vegetation types on Santa Cruz. Numbers for species associations correspond with those used in the text.

	Name in Wiggins & Porter	Matches in Beard's system	Predicted in Holdridge's system	Tree layer	Shrub layer	Herb layer	Species associations
Deciduous forest	Arid Zone vegetation	Deciduous seasonal forest	Thorn woodland	To 10 m high, deciduous, closed or open, some lichen epiphytes	Cover ± 70%, deciduous or evergreen sclerophyll	Strongly seasonal, therophytes dominate	Ia Ib
Semideciduous forest	Transition Zone vegetation	Semi-evergreen seasonal forest	No climatic data	15 m tall, semideciduous, some epiphytic bryophytes and ferns	Cover 70–80%, branches weak, often tangled	Seasonal chamaephytes dominate	IIa1
Closed evergreen forest	*Scalesia* Zone vegetation	± montane thicket	Premontane dry/moist forest	To 15 m tall, closed, epiphytes common	Cover 50–80%, most species erect	Nearly closed, not seasonal	IIa2 IIa3 IIb1
Open evergreen forest	Regarded as subdivision of *Miconia* Zone (Brown Zone)	Intermediate montane thicket & elfin woodland	No climatic data	To 8 m tall, open forest, epiphytes very common	Open or closed	Open, less well developed than in closed evergreen forest	IIb2
Mossy evergreen scrub	*Miconia* Zone vegetation	Elfin woodland	Premontane moist forest	Absent	Closed, epiphytic bryophytes common, vascular epiphyte not common	Closed, dominated by ferns	IIc
Evergreen herbaceous vegetation	Fern-Sedge Zone vegetation	No counterpart	Premontane moist (wet) forest	Absent	Absent	Closed	IId

The success of introduced trees with efficient dispersal on the upper slopes of Santa Cruz (and on other islands) indicates that the absence of native forests in these localities is a consequence of the fact that none of the native tree species will grow under the climatic conditions found on the wet slopes. Table 3 shows that most native trees on Santa Cruz grow in coastal and arid habitats and that the number of tree species decreases in wetter habitats. It is, no doubt, not difficult to introduce a number of tree species that could convert the treeless upper slopes of Santa Cruz into a forest, as several already introduced species are threatening to do. The fern flora on the upper slopes of Santa Cruz Island also suggests that the habitat conditions are not extreme compared with the American

continent. Because the degree of endemism among ferns is much lower than among flowering plants, and because ferns are, in general, capable of effective long-distance dispersal and are usually well represented on oceanic islands (Tryon, 1970), they are potentially very useful for comparing habitat conditions between islands and continental areas. A survey of the ferns and fern allies (106 species have been reported from the Galápagos) shows that groups that characterize extreme conditions on the American continent are generally lacking in the Galápagos. Examples are the absence of groups indicative for nutrient-poor soils, such as *Lindsaea* and *Schizaea*, or groups such as *Eriosorus, Jamesonia* and *Jamesonia* look-alikes (e.g., *Gleichenia simplex* and *Grammitis moniliformis*) growing in scrub just below the paramo, where a combination of low temperature and high humidity limits tree growth. Instead, the dominating ferns in the wettest habitats on Santa Cruz Island are such widespread, weedy species as *Pteridium aquilinum, Blechnum polypodioides, Lycopodium reflexum, Pityrogramma calomelanos,* and *Thelypteris oligocarpa*. My fieldwork in continental Ecuador, Peru, Venezuela, and Panama has shown that fern species associations on the Galápagos are similar to those on the mainland (although the number of species is lower) and that each species occupies a similar habitat on the Galápagos as on the mainland. There are a few exceptions, such as the presence of *Ophioglossum reticulatum* in dry vegetation on Alcedo, or that *Ophioglossum palmatum* is terrestrial on its only station in the Galápagos and not epiphytic as elsewhere. Unfortunately, there are few publications listing fern habitats and their fern species; some data from tropical South America are presented in Tryon, 1960 (Peru) and van der Werff & Smith, 1980 (Edo. Falcón, Venezuela).

Based on a comparison between flora (including pteridophytes) and vegetation structure on the Galápagos archipelago and the American continent the following conclusions can be drawn: A) The Galápagos archipelago is very poor in species; B) Many of the native species show weedy characteristics and the vegetation types composed of these species show secondary characteristics (short life span of the dominating species, simple structure and absence or low number of such specialized vegetation structures as lianas, epiphytes and a deep shade-tolerant herb or shrub layer); and C) There is a virtual absence of the main building blocks of primary vegetation, long-living, large trees (especially in the more mesic habitats, Table 3). This absence of long-living trees has given the undisturbed (primary) vegetation types on the Galápagos their secondary characteristics. The most likely explanation for the very low number of tree species on the Galápagos is that diaspores of tree species have not managed to cross the 500 miles separating the Galápagos from the mainland. As human-introduced species have shown, long-living trees can grow very well in the Galápagos; they would, if left uncontrolled, change the vegetation of the mesic interior of the islands in evergreen forests. Thanks to the dedication of the Ecuadorian National Park Service, the peculiar primary vegetation types with secondary characteristics (as the *Scalesia* forest, the *Miconia* scrub, and the pampa vegetation) are still more or less intact, waiting as it were for the arrival (not introduction by humans) of tree species with primary forest characteristics.

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SATELLITE IMAGES: A TOOL IN VEGETATION STUDIES, CONSERVATION, AND MANAGEMENT IN GALAPAGOS[1]

Marlene Meyer and Henning Adsersen[2]

ABSTRACT

Computerized analysis of multispectral satellite images can be used for mapping and monitoring vegetational changes due to climatological changes and introduced organisms. Vegetation can be classified by use of a vegetation index. Two examples from Galápagos are considered.

The use of satellite images is a technique within the field of remote sensing, which is "observation of a target by a device some distance away from it" (Barrett & Curtis, 1982). In addition to satellite images, remote sensing involves aerial photos, echosounding, radar, sonar, and magnetic measurement.

The use of satellite images is still in a stage of technical development, although many applications have already proved useful. It is relevant wherever data of the surface and atmosphere are needed, as in meteorology and geology. In studies of vegetation, satellite images have been used in soil and land-use surveys, in conservation and resource management, in desertification assessment (Barrett & Curtis, 1982; Olsson, 1985). Several satellites have been launched in recent years, e.g., LANDSAT, NIMBUS, NOAA, COSMOS, METEOR, and SPOT. This paper deals mainly with the LANDSAT system.

The images used here, taken in March 1979, are from the LANDSAT 3, which was launched in 1978. It operated in a sun-synchronous near-polar orbit at an altitude of 915 km. The satellite circled the earth every 103 minutes, and the acquired imagery covers the entire earth every 18 days.

LANDSAT satellites carry several kinds of sensors, all recording within the visible and near-infrared region of the electromagnetic spectrum. The "return beam vidicon camera system" (RBV) operates in the range of 0.51–0.75 μm while the multispectral scanner (MSS) is sensing reflected sunlight in four spectral bands from 0.5 to 1.1 μm (Table 1).

The next step in the LANDSAT program, the LANDSAT 4–5, also includes the Thematic Mapper (TM), which consists of six bands, ranging from 0.45 to 12.5 μm, including three visible, a near-infrared, a mid-infrared, and a thermal-infrared band (Barrett & Curtis, 1982).

Products of the LANDSAT satellites are available in digital and photographic forms. Digital products come as computer-compatible tapes. Each tape contains one scene in digital form. A scene covers an area of approximately 185 × 185 km. The size of the area on the ground (footprint) represented by one picture element (pixel) in the image is 57 × 57 m. The pixel size differs from

[1]We thank the staffs of the Charles Darwin Research Station and the Galápagos National Service for help and hospitality April–June 1987. A special thanks to Jonas Lawesson, who invited M. Meyer to participate in fieldwork sponsored by the Danish Natural Science Research Council. The expenses of our stay and participation in the workshop were covered by Julie von Müllen's Foundation and the Danish National Space Agency through a grant to Henning Adsersen.

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TABLE 1. Spectral bands of LANDSAT 3 MSS.

Band	Wavelengths (μm)	Spectral regions
4	0.5–0.6	visible green
5	0.6–0.7	visible red
6	0.7–0.8	near infrared
7	0.8–1.1	near infrared

FIGURE 1. LANDSAT 3 scene of northwestern part of Galápagos.

scanner to scanner. The Thematic Mapper produces images with a pixel size of 30 × 30 m, while the pixel size of the European satellite SPOT is 20 × 20 m in 3-band mode. Figure 1 shows band 4, of a scene covering the northwestern part of the Galápagos.

For each spectral band, each pixel holds a pixel value or gray-level value ranging from 0 to 127 (LANDSAT 3), indicating the amount of reflected sunlight from the footprint area. Figure 2 shows a histogram illustrating a typical distribution of pixel values in band 2.

The different types of surfaces in a scene, such as rock, water, soil, and vegetation, show distinctive patterns in each band, so-called spectral signatures. Figure 3 shows the spectral signatures of vegetation, soil, and water.

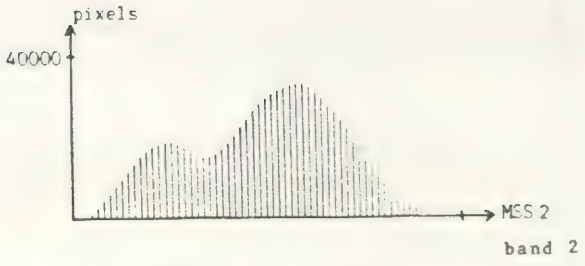

FIGURE 2. Histogram of pixel values, band 2.

DIGITAL IMAGES PROCESSING

Any one scene consists of approximately 7 million pixels in each band. It is clear that handling and analysis of so many data call for special computer facilities. The images in this paper were processed at the image processing system "EBBA II," which was developed by the Swedish Space Corporation. The facilities are located on The Institute of Geography at The University of Copenhagen.

Before thematic analysis takes place, preprocessing of the images is needed. A geometrical correction is made in order to fit the image to the chosen map coordinate system (Niblack, 1985). And sub-images of 512 × 512 pixels are extracted; this is the maximum image size that can be monitored at the screen.

The software enables the analyst to carry out several kinds of classification and to create false-color images in which each color represents a class.

The simplest kind of classification is based on one band. The histogram of 127 gray levels is divided into intervals, each representing a class. As the gray levels in each class often overlap, this type of classification is seldom satisfying. Most often multispectral classification—the combination of several bands—is needed to distinguish classes. Figure 4 illustrates the principle in classification using two bands, in a so-called scattergram. When classification is based on more than two bands, statistical methods like maximum-likelihood classification can be used.

The purpose of digital image processing is often to classify crops, vegetation, or other resources in areas too large to be covered by normal ground-based fieldwork. The procedure is to define small and well-known test areas and then to train the computer to find similar areas with the same spectral signatures pattern. This is called supervised classification (Schowengerdt, 1983).

VEGETATION IDENTIFICATION AND CLASSIFICATION

Vegetation is the basic productive and physiognomic element in all terrestrial ecosystems, natural ones as well as those under exploitation or cultivation. The study of vegetation types and their distributions is thus essential not only within ecology, but also within disciplines related to management or exploitation of natural sustainable resources.

While the great advantage of satellite images is that they offer frequent and exact data of large areas, the restriction is the size of the pixels. Studies on vegetation can be carried out on the level of vegetation types but is seldom possible on community or species level.

The spectral signature of vegetation shows a very distinct pattern (Fig. 5). Chlorophyll absorbs radiation in the visible green part of the spectrum, while the reflection is high in the near infrared part of the spectrum. These spectral intervals are represented by bands 5 and 7 respectively. A

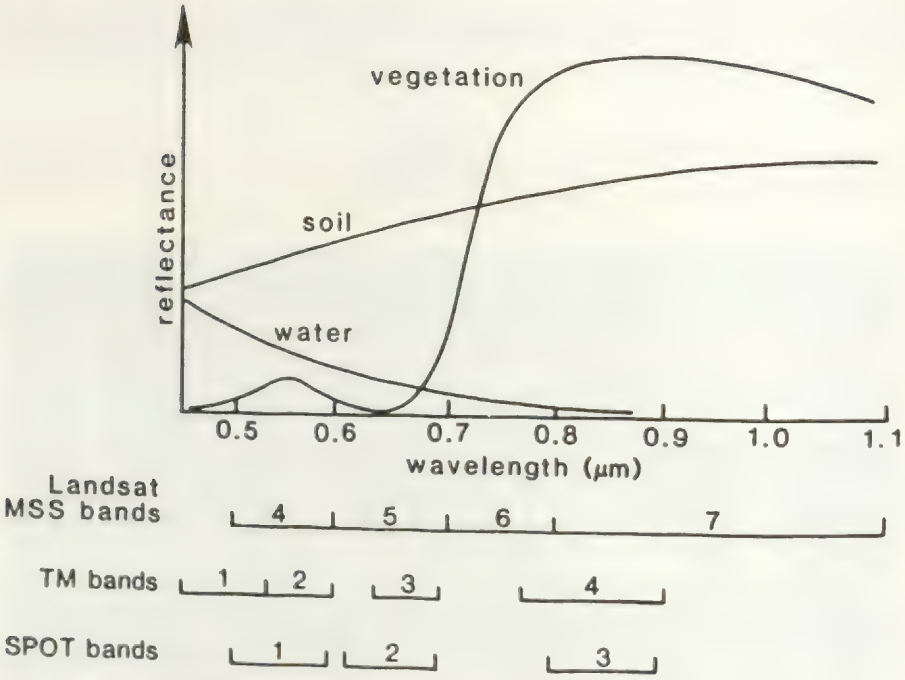

FIGURE 3. Spectral signatures of vegetation, soil, and water, and the recorded spectral bands of the LANDSAT Multispectral Scanner (MSS); the LANDSAT Thematic Mapper (TM); and the spot satellite (from Olsson, 1985).

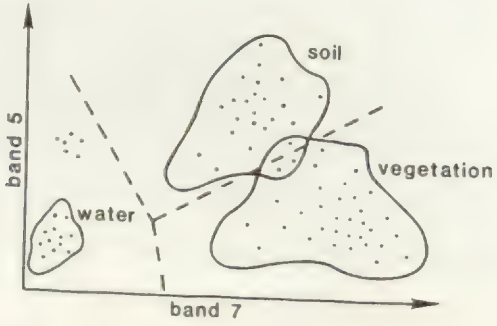

FIGURE 4. Two-band scattergram (Schowengerdt, 1983).

transformed ratio between the two bands, a so-called vegetation index (VI), therefore illustrates the "greenness" or chlorophyll contents in the vegetation cover. VI is defined as (Olsson, 1985):

$$VI = \left(\frac{b7 - b5}{b7 + b5} + 1\right) 100$$

(b5 and b7 being the gray level in band 5 and 7, respectively). The linearly transformed vegetation index forms a new "band," with gray levels ranging from 0 to 200. Classification is made by

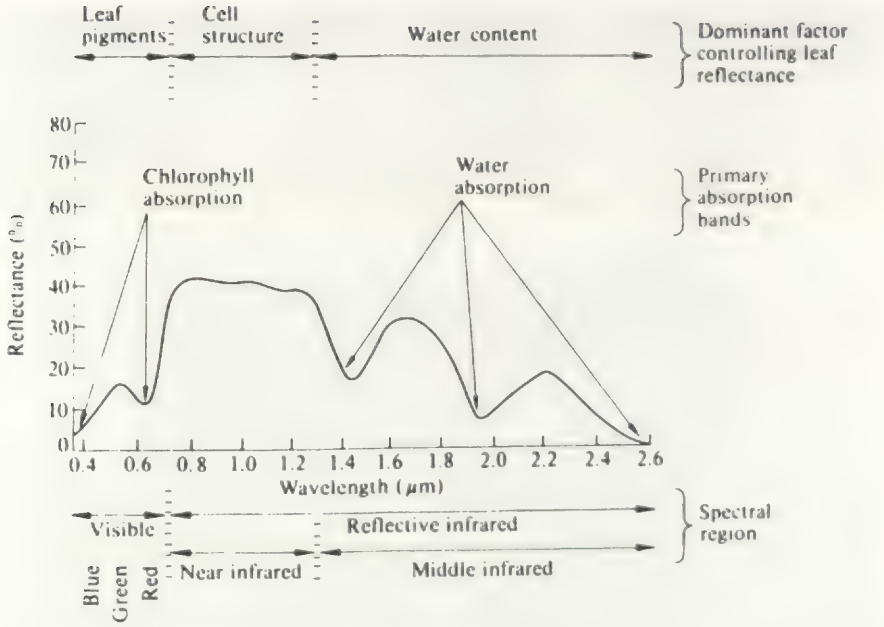

FIGURE 5. Spectral signatures of vegetation (from Olsson, 1985).

dividing the histogram of gray levels into intervals. The problem is to define the intervals so that they form classes that correspond to real differences in the vegetation. The result will then depend on the quality of the data of the test areas. As shown in the examples below, vegetation can be classified roughly by the vegetation index, i.e., using only two bands and one scene.

Studies in other parts of the world have shown that seasonal changes in the spectral signatures of vegetation offer more accurate differentiation of vegetation types, revealing even species stands or crops. Such multitemporal analyses require several recordings of good quality within the same growing season (Rasmussen, 1982). In Galápagos, where seasonality is one of the most important factors for vegetation zonation, such methods may prove powerful.

TWO EXAMPLES FROM GALAPAGOS

Figure 6 shows Volcán Alcedo at Isabela, illustrating classification using the vegetation index. The darkest tones correspond to the two classes with the highest VI.

Water and clouds are classified by gray levels in band 4. A "clean-up" has been made in order to remove erroneously classified single pixels. This image is made to demonstrate the principle of VI classification. The classes could be subdivided in order to make the images more detailed, but cannot be illustrated in black and white, since the number of classes that the human eye can distinguish is a limited number of tones.

Volcán Alcedo is the botanically best examined volcano due to the studies of van der Werff (1978). We have used his descriptions to verify our classification. It should be stressed that this type of ground data is not ideal, as it was not intended to be used in satellite imaging. Collecting of data for this purpose would focus more on spatial distributions of the classes. Van der Werff recognized the structural types listed in Table 2, but his indications of where the different types are found are

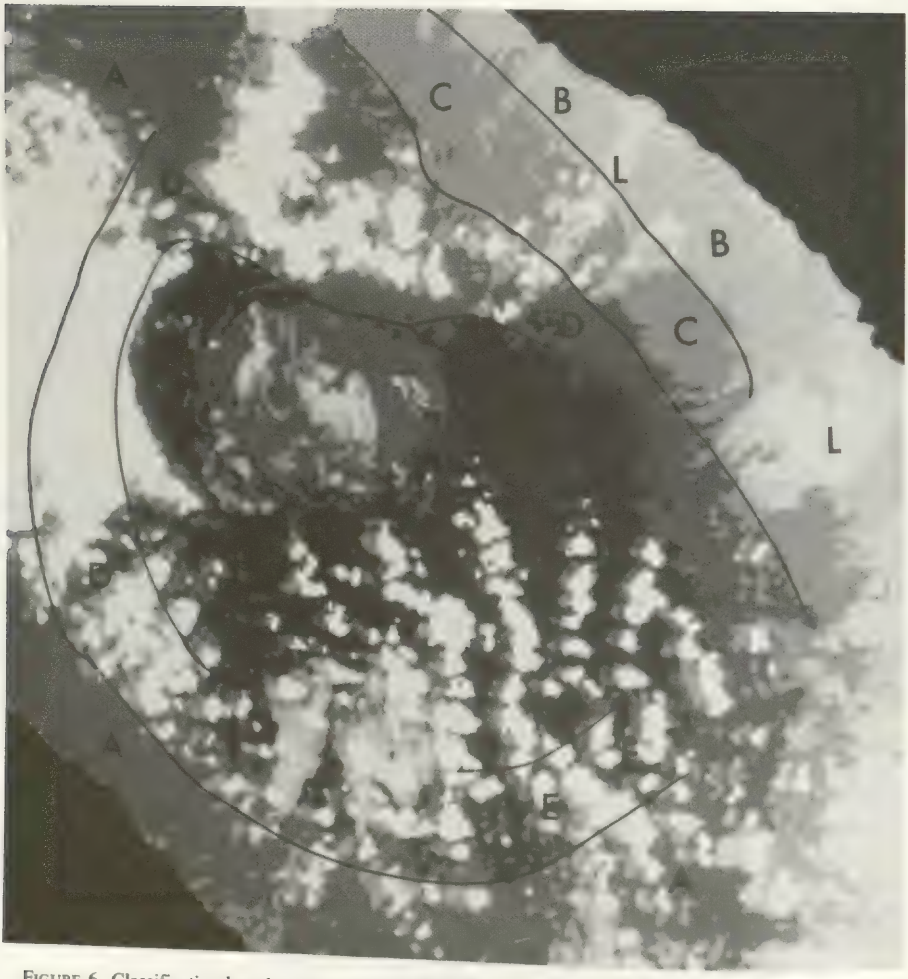

FIGURE 6. Classification based on vegetation index, Volcán Alcedo. Letters correspond to van der Werff's classification. (See Table 2.)

made in general terms (e.g., western slope, coast to 300 m elevation for type A). Furthermore, the altitude indications on the existing map (hydrographic charts, U.S.) are not precise. Nevertheless, we have tried to mark the most important altitudinal limits according to van der Werff, and according to field notes from a brief visit to Volcán Alcedo by H. A. in 1974.

There is no problem in identifying the dry vegetation types of the low altitudes (types A–E). Van der Werff's altitudinal limits agree remarkably with the classification on the satellite image. It proved more difficult to localize the types confined to the high altitudes, but the vegetation types here are all evergreen, and high-altitude images are complicated by clouds and cloud shadows.

To get a closer look on central Alcedo we extracted a sub-image showing the caldera and the southeastern slope (Fig. 7). The darkest vegetation class in Figure 6 is here divided into three different classes to give a more detailed picture of the vegetation. The complexity of the vegetation mosaic as described by van der Werff is evident. Classes D and F can be distinguished, and two additional classes can be recognized. Field data may allow determination of the distributions of types G–K.

TABLE 2. Structural vegetation types as recognized by van der Werff (1978), according to the system of Fosberg (1967).

A: Dry-season deciduous forest
B: Evergreen orthophyll shrub savanna
C: Deciduous orthophyll shrub savanna
D: Open evergreen orthophyll shrub savanna
E: Dry-season semideciduous forest
F: Broad-leaf evergreen orthophyll
G: Evergreen orthophyll vine scrub
H: Megaphyllous evergreen orthophyll
I: Open evergreen soft-wood orthophyll
J: Open gnarled evergreen mossy forest
K: Evergreen fern meadow
L: Recent, vegetationless lava

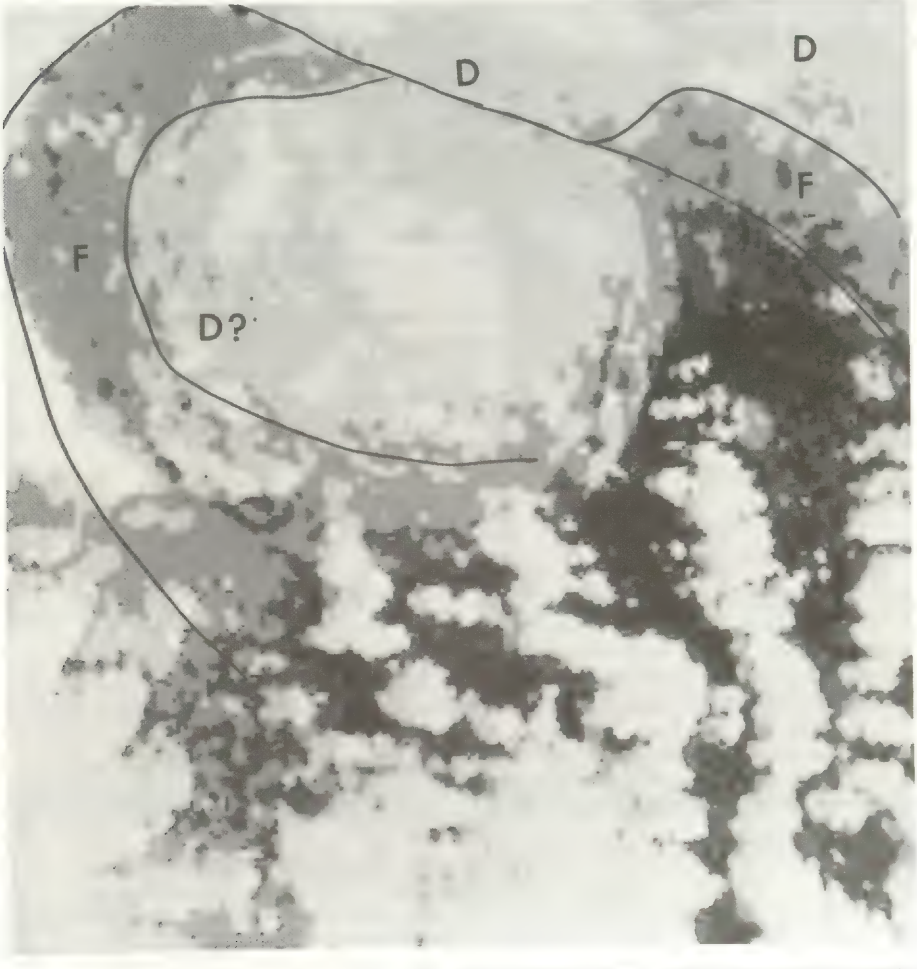

FIGURE 7. Classification based on vegetation index, Central Volcán Alcedo. Letters correspond to vegetation units in Table 2.

Applications on Galapagos

The Galápagos Archipelago is a good example of an area where satellite imaging has great potential in mapping and in studies of dynamics, especially because the topographical maps available are old and of poor quality, and they do not cover the whole archipelago (Sea charts, 1942, U.S.S. Bowditch). Moreover, Galápagos itself is quite isolated and most of the national park is difficult to access.

The variation of vegetation is great for an area of that size, and the basic knowledge of distributions is still scanty for some areas. Studies on vegetational distributions and on climate and soil remain to be made.

The Galápagos is characterized by instability. It is one of the most geologically active areas in the world (Simkin, 1984). Satellite imaging would be a suitable way to map new lava flows and to follow the recovery of vegetation.

Hard-copy satellite images from Galápagos have been employed in a vegetation mapping project carried out by the French organization ORSTROM in cooperation with national and local agencies. The maps are close to publication (C. Huttel, pers. comm.) Also, the Clirsen Institute in Quito has published examples of satellite images from Galápagos (Sánchez, 1985).

The changes in vegetation patterns caused by climate are marked, not only seasonally but also from year to year (Colinvaux, 1984). Multitemporal analyses of vegetation would yield a better understanding of the phenology of Galápagos organisms.

On islands where introduced animals have been eradicated, the recovery of the native vegetation could be monitored (Hamann, 1984).

Introduced animals and plants are threatening part of the native flora and fauna. If the stands of the most invasive plants species like *Lantana camara* or *Psidium guajava* could be recognized on satellite images, it would be possible by means of multitemporal analysis to follow their spread or eradication.

For the dynamic aspect of vegetation formation the methods are equally applicable. At present, the revegetation of Sierra Negra's south slope after the disastrous fire in 1985 is being studied by means of permanent vegetation quadrats (Nowak et al., this volume). A project has been set up by the authors in which we intend to use satellite images to study the extension and dispersal of the vegetation types exemplified by the quadrats.

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MAPPING AND CLASSIFYING VEGETATION IN THE GALAPAGOS ISLANDS, SOME CONSIDERATIONS[1]

I. A. E. Atkinson[2]

ABSTRACT

Reasons are given for mapping the vegetation of the Galápagos Islands at scales of 1:50,000 or larger. Major constraints on such mapping at present are the lack of recent high-quality aerial photographs and lack of topographic maps at suitable scales. Adoption of a standard sampling procedure is advocated, and suggestions are made for choice of such procedures. A logical system for defining and naming mapping units is essential, even though a subjective or arbitrary component in delimiting mapping units is inescapable. If definition and naming of units is based on intrinsic definable properties of the vegetation, maximum freedom is retained for subsequent classification of the mapping units using whatever system is most suitable for an identified purpose. An example of such a naming system is applied to particular Galápagos communities.

Huttel (this volume) has described his 1:100,000 mapping of climatic zones and vegetation formations for the whole of the Galápagos Archipelago. This work also included 1:50,000 maps of climate, geomorphology, vegetation, soils, land use, and land capability in the agricultural zones of the four settled islands. These maps will be a valuable basis for a variety of further studies but, as Huttel recognized, more detailed mapping of the vegetation as a whole is needed, especially where the pattern is heterogeneous.

Many botanical studies have been made in the Galápagos Islands but vegetation mapping has not been a priority. This paper gives reasons why detailed vegetation maps are needed, outlines some principles and guidelines for achieving satisfactory maps, and discusses questions of naming and classifying vegetation on such oceanic islands as the Galápagos.

WHY ARE VEGETATION MAPS NEEDED FOR THE GALAPAGOS ISLANDS?

If we are to retain the biological diversity of the Galápagos Islands, we must recognize that the different kinds of vegetation present require different procedures for management and protection. It is therefore essential to know what kinds of vegetation are present and where each occurs. The simplest way to record and convey this information is with a vegetation map. At an appropriate scale, the map can show the distribution of widespread kinds of vegetation and can identify particular kinds, such as *Sphagnum* bogs, that may be threatened by humans' activities or by introduced organisms.

A second reason for detailed vegetation mapping is that it provides a basis for future monitoring

[1]My visit to the Galápagos Islands was made possible by financial assistance from the Charles Darwin Foundation. I am grateful to staff at the Charles Darwin Research Station, particularly Dr. Jonas Lawesson, Sylvia Harcourt, and Felipé Cruz for opportunities to do fieldwork on six islands of the group. I thank Mr. J. R. Leathwick for his critical comments on methodology and Mr. G. C. Kelly, Dr. D. R. Given, and Dr. W. Harris for critiques of the manuscript. I also thank Tessa Roach for typing the manuscript and Carolyn Powell for drawing the figure.

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of vegetation changes resulting from intrinsic factors and from introduced plants and animals (Dorp et al., 1985). Without knowing what changes are occurring and the causes of the changes it is more difficult to decide what should be protected. For example, should we protect *Pteridium* fernland on Santa Cruz Island or should we assist its replacement by *Miconia* scrub? Or should we do both in different places? A vegetation map facilitates intelligent discussion of such questions.

Vegetation maps provide necessary information for taxonomic, evolutionary, and ecological studies of terrestrial species of plants and animals in the islands. Such information is needed for habitat descriptions and for identifying areas most vulnerable to the spread of alien plants, such as *Cinchona succirubra* Pav. et Klotzsch or *Pennisetum purpureum* Schum.

By showing what is growing where, detailed vegetation maps can be used to assist in resolving conflicts of land use in the agricultural zone and in defining areas sensitive to overuse by people in the conservation zone (van der Meulen et al., 1985). They can also become the basis for derivative maps that focus attention on particular kinds of biological or management information. For example, the 1:100,000 map of the Chatham Islands in the New Zealand region (Kelly, 1983), shows the distribution and conservation ranking of remaining areas of indigenous vegetation there. It can be used to identify priority areas for preservation and areas where restorative action, such as fencing out introduced mammals, would be most cost-effective.

Repeated recording of vegetation in permanent quadrats often reliably measures successional changes, but is feasible only for small areas. A detailed vegetation map allows permanent quadrats to be sited in representative kinds of vegetation and thus allows the quadrat results to be extrapolated more reliably. Furthermore, vegetation boundaries, when mapped, stimulate questions about the reasons for these boundaries.

These are strong reasons for detailed mapping of native vegetation on any oceanic island of biological importance. In the case of the Galápagos Islands, one of the world's most significant natural areas, the argument for a systematic and thorough mapping of the vegetation is compelling.

Map Scales, Base Maps, and Aerial Photographs

Small-scale maps, such as the 1:1,000,000 vegetative cover map of New Zealand (Newsome, 1986), are useful for educational, correlative, and other purposes that require a broad view of large areas. However, they lack sufficient detail for site-specific scientific and management purposes. For the larger islands in the Galápagos a map scale of not less than 1:50,000 is required and for the smaller islands 1:25,000 or larger. Still larger scales are needed for special purposes, as for example, mapping heavily visited areas.

No contoured maps at a scale of 1:50,000 are available for the Galápagos. The U.S. Hydrographic Survey maps of 1942 (corrected to 1962) are at a scale of 1:60,000 with contours at 60-m vertical intervals. The coverage is incomplete: Santa Cruz, southern Isabela, and Española were not included. Publication of reliable topographic maps of all islands, now in preparation by the Ecuadorian military, is essential to provide a satisfactory base for vegetation maps.

Aerial photographs of high quality are also essential for production of accurate vegetation maps. The greater part of the Galápagos was photographed by the U.S. Air Force between 1959 and 1963 at scales of 1:50,000 to 1:60,000. Areas not covered, in some instances because of cloud, include the higher parts of southern Isabela, northern Santiago, northern Floreana, and southeastern San Cristóbal. More recent aerial photographs, taken since 1981, have generally not been of a satisfactory standard. When new photographs are available, the earlier photographs will in some places be invaluable for measuring vegetation changes since 1959–1963.

For a variety of purposes, complete coverage of the Galápagos Islands with high-quality aerial photographs at scales between 1:25,000 and 1:40,000 using the most modern techniques is urgently needed.

Sampling for Vegetation Mapping

Excepting very large-scale maps, sampling for vegetation mapping requires data from many small samples. Otherwise extensive areas may remain unsampled. In the Galápagos, mapping of vegetation is likely to be completed by a number of individuals or teams working over a period of time so standardized procedures are needed.

QUALITATIVE AND QUANTITATIVE SAMPLING

Most vegetation maps are based largely on qualitative sampling and incorporate information on height and abundance of the major dominant species where appropriate. Provided the vegetation is not too heterogeneous and that there are substantial differences in floristic composition or structure among the mapping units recognized, qualitative sampling is satisfactory and is by far the most rapid method. For this reason, qualitative sampling is likely to be the most efficient in recognizing vegetation differences associated with major divisions of habitat (Smartt et al., 1976).

Where vegetation is heterogeneous, often with three or more dominant species, or where differences in floristic composition or structure among mapping units are likely to be small, quantitative sampling is needed to help define the units. When reliance is placed on quantitative sampling it is important that it is not allowed to become an end in itself, divorced from general observations of the vegetation pattern.

In the Galápagos it appears that on some islands substantial areas could be mapped qualitatively from ground traverses, using modern aerial photographs. High-resolution satellite images, when available, are likely to speed mapping, provided sufficient well-chosen reference areas are used to relate vegetation boundaries observed on the ground to the class boundaries derived from satellite data.

There are also parts of the Galápagos Islands, especially in what has been described as the "transition zone" (Bowman, 1961), where quantitative sampling is needed to differentiate vegetation mapping units. Even in relatively homogeneous vegetation, areas easily mapped with qualitative sampling now may become more heterogeneous in the future. Thus when time permits, quantifying vegetation composition and structure at the time of mapping allows a more precise measure of future changes.

PATTERNS OF SAMPLING

It is important in sampling vegetation to avoid or minimize personal bias. Most of us prefer to sample some kinds of vegetation more than other kinds. Although random sampling is often used for restricted areas, a fully randomized procedure is inefficient for mapping larger areas; unless sample density is very high, it is easy to miss areas that should be sampled. Systematic sampling allows more even coverage of the area, and stratified unaligned systematic sampling (Smartt & Grainger, 1974) is likely to give greatest accuracy and efficiency in mapping.

In the Galápagos, systematic sampling could be achieved by following compass lines where slopes are gentle, contour lines where slopes are steep, the radii of circular landforms such as cinder cones, or the long axes of elongate landforms, such as discrete lava flows. However, it is important with any kind of systematic sampling to ensure that a pattern is followed that gives uniform representation over the area (Greig-Smith, 1983). Density of undergrowth or spininess of plants will sometimes necessitate cutting a narrow path along the route prescribed (avoiding damage to larger or rarer plants) in order to progress at a satisfactory rate.

Whatever pattern is chosen, the positions of sampling lines should be decided and marked on a transparent overlay of the aerial photograph before going into the field. To do otherwise is to risk

undersampling some kinds of vegetation because they are unpleasant or uninteresting. In planning the sampling pattern, aerial photographs should be examined for differences in texture (different "appearance classes") so that sampling lines can be planned to cover these differences. This may result in an irregular arrangement of the sample lines but will ensure that all kinds of vegetation present are sampled.

SPACING OF SAMPLES AND DENSITY OF SAMPLING

More heterogeneous vegetation requires a greater density of samples for adequate mapping. The extent of heterogeneity will often not be known until after sampling has begun. One sample per km^2 (100 ha) is sometimes adequate for extensive areas of closed homogeneous vegetation, but open lava flows with few plants can be sampled at a lower density. When vegetation with several dominant species necessitates a higher sampling density, additional sampling lines can be interpolated between those already completed.

The most practical ways to space samples systematically along the sample lines are to count fixed numbers of paces (e.g., 100, 200, etc.) to each sample point or to use a hip chain. The latter device uses a reel of cotton run through a pulley on one's belt to measure distance. The counting of paces becomes automatic with practice and, although pace length is influenced by slope and microtopography, the number of paces can be increased for steeper slopes and microtopography introduces a random element to the sampling. Strict stratified-random or stratified-unaligned systematic sampling is most easily achieved using a hip chain, but pacing the standard between-sample interval and then walking a further 1–20 paces beyond (the exact number of steps being taken from a table of random numbers) is a second option.

Although counting paces and measuring distances along sample lines may appear tiresome, it does minimize personal bias. Each kind of vegetation through which the sample line passes should have chances of being sampled that are proportional to the area occupied by each.

KINDS OF SAMPLES

The large area of land to be mapped in the Galápagos Islands means that the sampling method must give the information required in the shortest possible time. Quadrats and other kinds of sample plots that require marking boundaries are not suitable as the major source of mapping information. It is faster to use plotless sampling either for qualitative descriptions or for quantitative samples in which counts are made of relative numbers or relative percentage cover of the plants present. Sample size depends on the parameters being measured.

At each sampling site it is important to record: date, sample number, aerial photo number, altitude (in m), aspect (in quadrants), slope (in slope classes), physiography, parent material of soil if identifiable, drainage, human influence, presence and size range (2–20 mm; 20–200 mm; >200 mm diam.) of loose rocks on the surface if any, and presence or absence of bedrock such as lava at the surface. The height of the vegetation should also be recorded together with any other data required, e.g., damage by browsing mammals.

VEGETATION ATTRIBUTES, AND PARAMETERS USEFUL FOR MAPPING

Because the dominant plant species have so much influence on the structure and functioning of communities, it is logical to focus on these plants when choosing parameters for distinguishing mapping units. A useful extension of this idea is to sample all plant species that contribute to the uppermost layer of vegetation (canopy), whether these are dominant or rare species. The uppermost

vegetation layer or canopy can be at or near ground level in low-growing vegetation or tens of meters above it in forest.

The most commonly used qualitative attributes for species in the canopy are abundance (the relative number of individuals of a species in a defined area) and cover. Abundance of a species can be estimated in 2–5 classes, but estimates of abundance using more than three classes are not easily repeatable among observers. Percentage cover is sometimes estimated in classes spanning equal ranges, but a more repeatable procedure uses classes of unequal ranges and takes advantage of the fact that very small and very large cover percentages, and those near 50%, are easier to estimate, viz., 1–10%, 10–40%, 40–60%, 60–90%, and 90–100%. When time is very limited, enough information for mapping purposes can be obtained using four cover classes: 1–9%, 10–19%, 20–49%, and 50–100%. Qualitative cover estimates can be satisfactory for small areas (e.g., 4 m^2) but observer differences become increasingly large as the area of estimation is increased (cf. Sykes et al., 1983).

Frequency, relative density, and crown cover are quantitative parameters that can be measured rapidly when sampling the canopy.

Frequency. To record frequency with plotless samples, a circle of convenient radius (e.g., 3 m) can be estimated by eye from the sample center and a listing made of all canopy species within it. Although simple to measure, frequency has a low power of discrimination for mapping purposes: the frequency of major species from samples in very different kinds of vegetation can be similar.

Relative density. Relative density is the proportion contributed by a particular species to the total number of individuals of all species in a group. It can be obtained by counting fixed numbers of plants in the canopy, e.g., 25 or 50 individuals. Although useful in many forest and scrub communities, density measurements of any kind are of little value when it becomes difficult to count individual plants, e.g., thickets of *Clerodendrum molle* HBK or *Cryptocarpus pyriformis* HBK, grasslands of *Pennisetum purpureum* Schum., mossfields of *Sphagnum*, or communities dominated by lichens.

Crown cover. In mapping work it is not practical to record the percentage *leaf* cover because it is too time-consuming. Percentage *crown* cover is recorded instead. A plant crown includes all foliage borne by the plant; the vertical projection of this foliage volume onto the ground is measured as crown cover. For mapping purposes crown cover of canopy plants is measured. The most accurate and rapid method of measuring this is to use point quadrats where errors associated with the boundaries of the quadrat are reduced to zero (Greig-Smith, 1983). A point that intercepts a gap between leaves but is within the perimeter of the plant's effective crown is recorded as a crown intercept. Some plant crowns are made up of discrete segments, or are very asymmetrical in plain view because of their branching. The gaps between such segments are recorded as gaps (sky if sighting upward) in the same way as those that occur between individual plant crowns (Fig. 1).

Various methods of point analysis for crown cover are available. In vegetation less than 0.5 m high, a step-point method can be used (Evans & Love, 1957; Atkinson, 1962, 1985). In scrub or shrubland that is too short to walk beneath, a pointed stick rotated at arm's length and at right angles to the direction of travel can be used to obtain point intercepts (Atkinson, 1985).

A rapid method developed by the author, and apparently suitable for forest in the Galápagos Islands, is to use low-power binoculars to sight vertically upward into the canopy. The moment a vertical line of view is reached, the observer freezes that position, and identifies the species whose crown is at the center of the field of view. That the binoculars will not always be aimed vertically is much less important than achieving a consistent angle and hence an unbiased line of sight. Binoculars are preferable to other types of viewfinders since the magnification combined with the

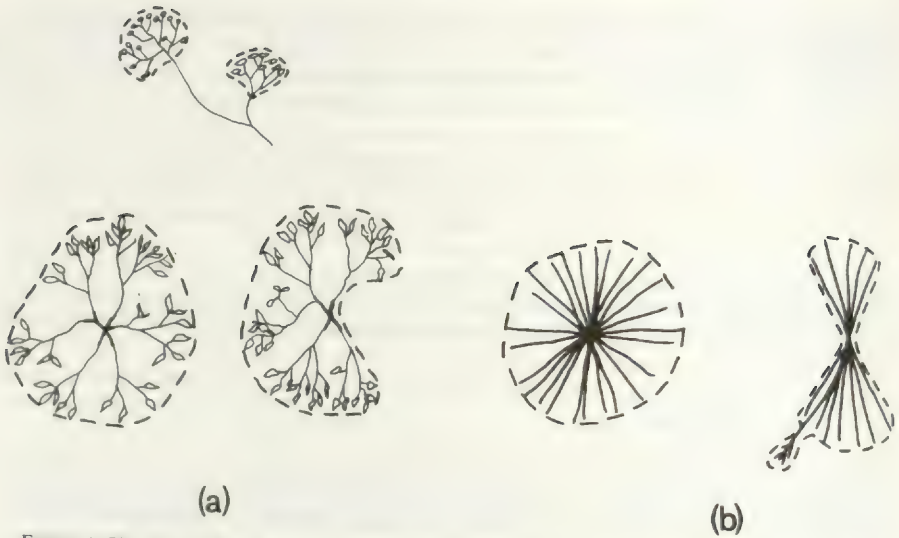

FIGURE 1. Plan views of (a) dicotyledon and (b) monocotyledon showing the limits of plant crowns (dashed lines) in plants with symmetrical and asymmetrical crowns. A point intercept within the dotted lines would be recorded as a "hit" for that particular species regardless of whether it intercepted an individual leaf. Point intercepts outside the dotted lines would be "misses" recorded as bare ground or sky depending on the direction of sighting.

ability to see those parts of the canopy immediately surrounding the sample point assists with identification of the species. The disadvantage is that if one allows the binoculars to move slightly *after* the position is frozen, there could be bias toward plants that the observer can identify most easily. This is not a problem in forests less than 15 m tall, and the height range of most Galápagos forests (4–7 m, Hamann, 1981), together with the restricted number of species, make the method suitable here.

Spacing of point intercepts at a sampling site can be randomized or systematic; systematic sampling is generally easier. A simple procedure at a sampling site is to record point intercepts at one-pace intervals in low vegetation, at two-pace intervals in vegetation 0.5–2.5 m high, and at intervals of five or ten paces in forest, depending on its height. At least 25 points should be recorded, and 50 points (in two parallel transects) in heterogeneous vegetation.

If point intercepts for sky and/or bare ground are recorded, the point analysis gives an estimate of the absolute cover for each species in the canopy and the total crown cover of this layer. The results are conveniently expressed as percentages. The advantages of relying on crown cover in the canopy for mapping vegetation are that it is quick to record, it can be measured in all types of terrestrial vegetation, it is a measure of what any observer sees from the outside, and it is easily definable as a baseline for measuring future change in the vegetation.

What should be done about measuring the crown cover of deciduous plants in the dry season? Tests by the writer in *Bursera graveolens* forest on Santa Cruz Island showed that, when leafless, the live twigs can be used to delimit the crown area. There will be errors associated with misidentifying dead wood as living twigs, but sampling the vegetation during the dry season when deciduous plants have lost their leaves should not present insuperable problems. However, the composition of the ground layer shows marked seasonal changes, particularly with respect to herbaceous plants.

MEASUREMENT OF SAMPLING ERROR

Sampling error arises from spatial variation in the composition of the vegetation sampled and from error in recording. If the former source of error does not exceed the latter, then the method of sampling is of little value.

Approximate 95% confidence limits for the sampling error associated with crown-cover estimates made during systematic sampling are given by the formula:

$$s = \sqrt{\frac{p(1-p)}{n}}$$

where s = the standard error of the estimate of the proportion (p) of a species based on a sample of n points obtained from a systematic sample (Williams, 1956; Atkinson, 1962). This relationship assumes that successive crown-cover samplings of an area of vegetation are binomially distributed. Greig-Smith (1983) provides more detailed discussion of sampling error.

Although theoretical calculations of sampling error can be made, it is more satisfactory to measure sampling error directly in the field with repeated sampling by the same observer at the same sample site. A 50-point sample repeated three times through the same stand gives a direct measure of sampling error and thus of the level of difference that is likely to be significant when comparing the composition of several stands. Differences between observers can also be measured by having two or more observers sample along the same line (Evans & Love, 1957).

The Relevance of Existing Botanical Data to Vegetation Mapping in the Galapagos

Information from the many quadrats, relevés, and other samples already made in the Galápagos Islands could be used in a mapping program, provided the samples can be located on a base map or aerial photograph. If estimates or measurements of cover are available, as for example in Hamann's (1981) study, it will sometimes be possible to use the samples to indicate the mapping units present. Where cover estimates are not available, the data can be used at a later stage (following delineation of the mapping units) to help describe the characteristics of the mapping units and their ranges of variation.

The Subjective Nature of Vegetation Mapping Units

Whether vegetation is sampled qualitatively or quantitatively, a choice must be made between fitting the sample data into a preexisting classification of mapping units derived from earlier general observations, the a priori approach, or whether to generate the mapping units largely from the sample data, the a posteriori approach (Küchler, 1967). The advantage of the first approach is that large numbers of general observations can readily be used to delimit the mapping units. The advantage of the second is that various sorting and clustering strategies can be applied to segregate mapping units that more closely depict the vegetation pattern. This way, unusual combinations of plants revealed by the sampling are less likely to be allocated to and lost within preconceived categories.

The above considerations underlie the essentially subjective nature of the process of delimiting mapping units, whether sampled qualitatively or quantitatively, and whether classified before or after the survey is completed. Although the apparent discreteness and repetitive stand composition of some biotic communities gives an illusion that they are self-replicating units comparable to

species, the reality is that biotic communities are composed of different species populations, each responding individually to environmental factors (Gleason, 1926). Insofar as environmental factors are continuous or discontinuous in their effects, so also will the resultant vegetation be continuous or discontinuous. The vegetation mapper takes advantage of perceived discontinuities on the ground in drawing the map but where variation is more continuous (for example, along gradients of altitude, slope, or water table), delimiting separate mapping units is an arbitrary, even though potentially repeatable, process.

Clustering Strategies for Delimiting Mapping Units

No particular strategy is needed to allocate samples to a preexisting classification of mapping units. If, however, mapping units are generated from qualitative samples, then simple criteria, such as structure or presence of certain dominant species, can be used to cluster samples and define the mapping units.

Use of quantitative samples to generate mapping units allows use of a variety of sorting and clustering strategies in defining mapping units. Principles of clustering and methods available are discussed by Clifford & Stephenson (1975) and by Gauch (1982). A method developed by Atkinson (1985) uses a clustering procedure that gives priority to combining similar samples that are physically closest together in the field. This allows class boundaries to be made more nearly coincidental with map boundaries.

A clustering strategy that is satisfactory for mapping purposes, whether using qualitative or quantitative data, should produce simple groups that reflect the most frequently occurring stands of vegetation in the field. Sample groups that contain only one or a very few samples often cannot be mapped at the chosen map scale. However, where such sample groups are of particular ecological interest in the Galápagos Islands, e.g., thermal sites, ponds, and bogs, a method should be sought to identify these sites on the map.

Deciding Boundary Positions on a Vegetation Map

When clearly visible in the field, vegetation boundaries will usually be apparent on aerial photographs. Such boundaries can be transferred directly to the map. The only restriction occurs when such boundaries separate areas too small to show at the chosen map scale.

Where spatial variation in vegetation is continuous there will usually be no clear vegetation boundaries, even though compositional differences between sample groups may suggest that a boundary should be drawn. Examples are gradational vegetation changes associated with gradients in altitude, depth or texture of volcanic ash, water table in weathered materials, and amounts of beach sand mixed with lava. However, causal factors for gradational changes observed will often not be known.

Any procedure for placing boundaries across gradations will be somewhat arbitrary but it need not necessarily be unrepeatable. Having identified the zone in which vegetation composition is most likely to be intermediate between that of the sample groups being separated, at least three ways of drawing boundaries can be used. The first is to use the contour at a particular chosen altitude. A second method is to use the upper or lower altitudinal limit of a selected plant species if such limits are readily recognizable in the field. Such limits are likely to change with aspect. The distributional limits of individual indicator species can be used in places where no altitudinal changes are involved. A third method is to use an easily recognizable topographic feature (stream channel, ridge crest, fault scarp). Using topography in this way may appear to be a departure from mapping the vegetation. This is not altogether the case because a decision to separate two areas will have already

been made on the basis of vegetation composition; topography is used only as a convenient way of locating the boundary.

Whatever method is used to locate boundaries in vegetation that shows continuous spatial variation, it is important for the mapper to specify the method(s) used. On the map, gradational boundaries can be distinguished from distinct boundaries by using broken rather than continuous lines.

Where vegetation stands of contrasting composition (A and B) occur together as a mosaic pattern, the differences may be at too small a scale to show on the map; then the contrasting stands can be described separately but shown on the map as a single unit labeled "A + B."

Classification and Naming of Vegetation Mapping Units

Delimiting mapping units is a classificatory process, even though no hierarchical relationship among the units need be used to draw the map. It is also a naming process; it is difficult to communicate information about the mapped vegetation pattern if the units are unnamed.

Mapping units are better named from specific, intrinsic, definable characteristics than from general names that convey inferences about the environments of the units. If this principle is followed, interpretations about the origin of the vegetation pattern do not become confused with description of the pattern itself. For this reason, I suggest avoiding such names as heath, steppe, savanna, desert, pampa, meadow, or swamp to vegetation at the mapping-unit level of classification. There is no reason to shun these terms if they are needed to express interpretations of the vegetation at a higher level of classification.

A widely used simple method of naming biotic communities and mapping units is to link the names of the dominant species with a physiognomic term that describes the kind of vegetation present, e.g., *Scalesia pedunculata* forest or *Macraea laricifolia–Bursera graveolens* scrub. This method will not work in floristically complex forests, such as those of South America, but it is particularly suitable for vegetation dominated by relatively few species as on the Galápagos Islands.

The principle of linking dominant species with physiognomic identity has been formalized in the naming system developed by Atkinson (1962, 1981, 1985), which can be applied to individual stands and to mapping units. Each mapping unit is given a two-part name. The first includes the species names of the leading species in the uppermost vegetation layer or canopy, and the second describes the structure of the vegetation based on the leading growth form. A canopy cover of 20% or more is a useful threshold value for the leading species to be used in the name. Where the canopy is of broadly similar although variable height, hyphens (–) are used to link species forming the canopy. Diagonal signs (/) are used to indicate that canopy species to the left of the sign are significantly taller than, or emergent above, those to the right. Physiognomically important species contributing less than 20% of the canopy cover can be used in the stand or mapping unit name. Such species are denoted by parentheses ( ) when contributing 10–19%, and square brackets [ ] for contributions under 10%.

When point analysis is used to measure crown cover it is easy to also obtain estimates of the percentage and kind of bare ground, which can be classified with respect to the texture of the ground surface. Such information can be used to characterize and name mapping units for open communities, such as those of very dry or young lava flows. Definitions of structural classes applicable to Galápagos vegetation are given in Table 1.

Examples of my application of this naming system to individual stands (rather than mapping units) sampled in the Galápagos Islands are shown in Tables 2 and 3. Table 4 uses Hamann's (1981) cover estimates to apply the same naming system to some of the communities sampled in his study. Hamann estimated the cover of individual vegetation layers separately rather than estimating the cover contributed by species for the uppermost vegetation layer regardless of their heights. Thus not all the floristic-structural names I have derived from Hamann's data (Table 4) are necessarily correct

TABLE 1. Diagnostic criteria for vegetation structural classes in the Galápagos Islands (modified from Atkinson, 1985) and definitions of growth forms.

Structural class	Diagnostic criteria for structural classes
1. Forest	Woody vegetation in which the cover of trees[1] and shrubs[1] in the canopy[2] is >80% and in which tree cover exceeds that of shrubs. Examples: *Psidium galapageium–Zanthoxylum fagara* forest and *Cinchona succirubra* forest.
2. Treeland	Vegetation in which the cover of trees in the canopy is 20–80%, with tree cover exceeding that of any other growth form, and in which the trees form a discontinuous upper canopy above either a lower canopy of predominantly nonwoody vegetation or of bare ground. (Note: vegetation consisting of trees above shrubs is classified as either forest or scrub, depending on the proportion of trees and shrubs in the canopy.) Example: *Bursera graveolens–Psidium galapageium* treeland.
3. Vineland	Vegetation in which the cover of unsupported woody vines[3] in the canopy is 20–100% and in which the cover of these vines exceeds that of any other growth form or bare ground. Example: *Rubus* vineland. Vegetation containing woody vines supported by trees or shrubs is classified as forest, scrub, or shrublands according to the proportion of trees and shrubs present.
4. Scrub	Woody vegetation in which the cover of shrubs and trees in the canopy is >80% and in which shrub cover exceeds that of trees (cf. Forest). Examples: *Scalesia pedunculata–Croton scouleri* scrub and *Lantana camara* scrub. (Note: To avoid confusion with shrubland, the term scrubland is not used in this classification.)
5. Shrubland	Vegetation in which the cover of shrubs in the canopy is 20–80% and in which the shrub cover exceeds that of any other growth form or bare ground. Example: *Castela galapageia* shrubland.
6. Fernland	Vegetation in which the cover of ferns in the canopy is 20–100% and in which the fern cover exceeds that of any other growth form or bare ground. Example: *Pteridium aquilinum* fernland. Tree ferns ≥10 cm dbh are classified as trees[1].
7. Grassland	Vegetation in which the cover of grasses in the canopy is 20–100% and in which the grass cover exceeds that of any other growth form or bare ground. Example: *Pennisetum purpureum* grassland.
8. Sedgeland	Vegetation in which the cover of sedges in the canopy is 20–100% and in which the sedge cover exceeds that of any other growth form or bare ground. Example: *Rhynchospora corymbosa* sedgeland.
9. Herbfield	Vegetation in which the cover of herbs[4] in the canopy is 20–100% and in which the herb cover exceeds that of any other growth form or bare ground. Example: *Blainvillea dichotoma* herbfield.
10. Mossfield	Vegetation in which the cover of mosses in the canopy is 20–100% and in which the moss cover exceeds that of any other growth form or bare ground. Example: *Sphagnum cuspidatum* mossfield.
11. Lichenfield	Vegetation in which the cover of lichens in the canopy is 20–100% and in which the lichen cover exceeds that of any other growth form or bare ground. Example: *Rocella portentosa* lichenfield.
12. Rockland	Land in which the area of bare basement rock exceeds the area covered by any one class of plant growth form. Cliff vegetation often includes rockland. When plant cover ≥1% rocklands can be named from the leading plant species. Example: *Chamaesyce* rockland.
13. Boulderfield, Stonefield, Gravelfield	Land in which the area of loose bare boulders (>200 mm diam.), stones (20–200 mm diam.), or gravel (2–20 mm diam.) exceeds the area covered by any one class of plant growth form. The appropriate name is given depending on whether boulders, stones, or gravel occupy the greatest area of land surface. Where plant cover ≥1% these openlands can be named from the leading plant species. Example: *Tiquilia* gravelfield.
14. Sandfield	Land in which the area of bare sand (0.02–2 mm diam.) exceeds the area covered by any one class of plant growth form. Dune vegetation usually includes sandfields, which are named from the leading plant species when plant cover ≥1%. Example: *Ipomoea pes-caprae* sandfield.

TABLE 1. Continued.

Structural class	Diagnostic criteria for structural classes
15. Loamfield, Clayfield, Peatfield, etc.	Land in which the area of bare soil, peat, etc., exceeds the area covered by any one class of plant growth form. The appropriate name is given depending on the surface texture of the material forming the bare ground.

[1]Trees are defined as woody plants (excluding vines) ≥10 cm diameter breast height (dbh). Shrubs are defined as woody plants (excluding vines) <10 cm dbh. Tree ferns ≥10 cm dbh are treated as trees. A height limit of 5 m may be a more useful criterion for separating shrub-size *Opuntia* sp. from tree forms but general application of this height limit fails to distinguish very old short trees from younger shrub forms.

[2]Canopy is defined as the layer or layers formed by the uppermost plant crowns or their parts and is applicable to any kind of terrestrial vegetation, whether herbaceous or woody.

[3]Herbaceous vines are treated as herbs in this classification.

[4]Herbs include all herbaceous plants except ferns, grasses, and sedges.

in terms of the present paper. However, these examples, together with communities sampled and named in Tables 2 and 3 give an idea of how this naming system would look if applied to vegetation mapping in the Galápagos.

Whatever naming system is adopted, it should be based on definable criteria and be internally consistent. Achievement of this will make it simpler to compare vegetation maps from different islands and thus facilitate the transfer of appropriate management strategies.

Criteria for classifying vegetation are discussed by Fosberg (1967), Whittaker (1975), and Mueller-Dombois (1984). As all these authors pointed out, there is no single "correct" classification suitable for all purposes. We may wish to emphasize physiognomy, floristic composition, life forms, geographical location, environmental factors, successional status, or conservation values in the classification. If, however, the initial delimitation of mapping units is based on intrinsic definable characteristics of the vegetation, then freedom is retained to choose whichever kind of classification best suits our purpose.

DISCUSSION

Physical difficulties of field sampling for vegetation mapping in the Galápagos Islands are associated mainly with the hot and sometimes humid climate, uneven lava terrain, spiny vegetation, and fire ants (*Wasmannia auropunctata*). None of these difficulties are insuperable, especially as substantial areas of the archipelago have rather even slopes devoid of the deep gullies and chasms so often present on islands with higher rainfall.

Galápagos vegetation is generally of short stature, and dominance by a small number of species is common. This makes a "dominance-type" approach to mapping straightforward but occasionally this does not usefully differentiate mapping units. If so, it will be necessary to sample the undergrowth so that diagnostic species other than those in the canopy can be used to separate mapping units.

Seasonal changes in vegetation in the Galápagos Islands are very marked, and ideally a description of a mapping unit should be based on sampling in wet and in dry seasons. The vegetation reaches maximum expression in the wet season, suggesting that preference should be given to sampling then. Dr. Huttel (pers. comm.) has suggested that, when the information is available, both wet- and dry-season vegetation composition could be shown in the mapping unit name, e.g.:

$$\frac{\text{Wet: (prickly pear–palo santo) / blainvillea herbfield}}{\text{Dry: (prickly pear–palo santo) / native lantana shrubland}} \quad \text{(see Table 2)}$$

TABLE 2. Examples of the use of a floristic-structural system to name communities (Atkinson, 1985) sampled on Santa Cruz and Santa Fé islands, Galápagos Archipelago (sampled April 1987).

Locality sample sizes, or sampling notes	Point analyses of crown-cover in the canopy: Growth forms and characteristic species	Total % cover	Scientific name of community	Common name of community
	(i) RIDGES			
Academy Bay, Santa Cruz (10 m)	trees (*Jasminocereus:* 10%)	22	(*Jasminocereus thouarsii*)/*Cryptocarpus pyriformis* scrub[1]	(Candelabro)/montesalado scrub[1]
(i) N = 50	shrubs (*Cryptocarpus:* 32%)	48		
(ii) N = 50	woody vines (14%), boulders (14%), herbs (2%)	30		
	(ii) HOLLOWS			
	trees	12		
	shrubs (*Cryptocarpus:* 70%)	82	*Cryptocarpus pyriformis* scrub	Montesalado scrub
	rocks, herbs	6		
Conway Bay, Santa Cruz (10 m)	trees (*Bursera graveolens:* 60%)	60	*Bursera graveolens* forest	Palo Santo forest
N = 25	shrubs (*Gossypium barbadense:* 12%)	24		
	woody vines, grasses, herbs	16		
	(i)			
Santa Fé (100 m)	trees (*Opuntia:* 14%; *Bursera:* 12%)	26	(*Opuntia echios–Bursera graveolens*)/*Blainvillea dichotoma* herbfield[1]	(Prickly pear–palo santo)/*Blainvillea* herbfield[1]
(i) N = 50	shrubs (*Cordia:* 10%; *Croton:* 10%)	22		
(ii) not sampled	herbs (*Blainvillea:* 22%)	34		
	grasses, dead trees, boulders	18		
	(ii)			
			(*Opuntia echios–Bursera graveolens*)/*Lantana peduncularis* shrubland[2]	(Prickly-pear–palo santo)/native lantana shrubland[2]
South slope, Santa Cruz (ca. 200 m)	trees (*Psidium galapageium, Zanthoxylum*)	40	*Psidium galapageium*/*Pennisetum purpureum* grassland	Guayabillo/elephant-grass grassland
Qualitative estimate	grasses (*Pennisetum purpureum*)	60		
South slope, Santa Cruz (ca. 600 m)	shrubs (*Miconia*)	100	*Miconia robinsoniana* scrub	Cacaotillo scrub
Qualitative estimate				
South slope, Santa Cruz (ca. 600 m)	ferns (*Pteridium*)	85	*Pteridium aquilinum* fernland	Bracken fernland
Qualitative estimate	shrubs (*Miconia*)	15		
North slope, Santa Cruz (ca. 650 m)	trees (*Scalesia, Zanthoxylum*)	40	*Scalesia pedunculata* forest	Lechosa forest
Qualitative estimate	shrubs (including *Scalesia*)	30		
	herbs	30		

[1]The first part of a community name is derived from the names of species that contribute 20% or more to the canopy cover. Conspicuous species with cover values less than 20% can also be used to name the community by enclosing their names in brackets (see text).

[2]Dead undergrowth of *Lantana peduncularis* was very prominent at the sampling site, indicating that at a different season the community would have been described as a shrubland.

TABLE 3. Naming of communities (following Atkinson, 1985) along an altitudinal gradient of a northwest slope on Santiago Island, Galápagos Archipelago. (Sampling route begins north of Buccaneer Cove; sampled 4 April 1987; N = 25/sample).

	Point analyses of crown-cover in the canopy			
Altitudinal range (m)	Growth forms and characteristic species	Total % cover	Scientific name of community	Common name of community
10–60	trees (*Cordia:* 4%)	4	*Croton scouleri*/ ?herbfield[1]	Chala/?herbfield[1]
	shrubs (*Croton:* 20%; *Castela:* 12%)	32		
	grasses	20		
	herbs	44		
100–150	trees (*Bursera:* 8%; *Cordia:* 8%)	16	*Blainvillea dichotoma* herbfield	*Blainvillea herbfield*
	shrubs	8		
	grasses	20		
	herbs (*Blainvillea* 40%)	56		
240–300	trees (*Bursera:* 28%)	36		
	shrubs	4	*Bursera graveolens*/ *Blainvillea*	*Palo santo*/*Blainvillea* herbfield
	herbs (*Blainvillea:* 40%)	60	*dichotoma* herbfield	
400–450	trees (*Bursera:* 40%; *Psidium:* 24%)	68	*Bursera graveolens*–*Psidium*	Palo santo–guayabillo treeland
	woody vines	4	*galapageium* treeland	
	herbs	28		
540–600	trees (*Bursera:* 12%; *Psidium:* 48%)	60	*Psidium galapageium* treeland	Guayabillo treeland
	woody vines	12		
	herbs	28		
670–770	trees (*Bursera:* 8%; *Psidium:* 24%)	52	*Psidium galapageium treeland*	Guayabillo treeland
	shrubs	4		
	woody vines	4		
	grasses, herbs	40		
800–850	Not sampled	—	? herbfield[1]	? herbfield[1]

[1]Herb species not identified in sample.

Whatever naming system is adopted, the advantages of using common names (when available) for plant species included in the unit names are that they are often shorter, they do not change with taxonomic revisions, and they help people other than botanists understand and use the maps.

The predominance of treeland in the samples from Santiago Island (Table 3) is apparently related to the killing of young trees by goats and pigs. Small stands of forest (with >80% canopy cover of trees and shrubs) were seen but were too small to appear in the sampling. The vegetation of Santiago shows all stages of structural degradation induced by goats: forest → treeland → herbfield or grassland. On Santa Fé Island, the low value for crown cover of *Opuntia echios* in the canopy, especially when compared with that of *O. echios* on the small island seaward of the usual anchorage, can probably also be related to the former presence of goats on the main island up to 1971.

This paper stresses mapping scales between 1:25,000 and 1:50,000. Larger-scale maps of the more intensively visited parts of the Galápagos Islands, coupled with fixed-point photography, would provide a more adequate basis for monitoring changes.

TABLE 4. Application of a floristic–structural naming system (Atkinson, 1985) to vegetation in the Galápagos Islands. (Some examples drawn from Hamann, 1981).

Site number	Island	Leading species and formation class names used by Hamann (1981)	Floristic–structural name derived from cover estimates of Hamann (1981) and from criteria of the present paper
1	Santa Cruz	*Cryptocarpus pyriformis* scrub	*Cryptocarpus pyriformis* scrub
2	Santa Cruz	*Opuntia echios–Croton scouleri* steppe forest	*Opuntia echios/Croton scouleri* forest[1]
3	Santa Cruz	*Pisonia floribunda–Piscidia carthagenensis–Opuntia echios* forest	*P. floribunda–(P. carthagenensis–O. echios)* forest[2]
29	Santa Cruz	*Psidium galapageium–Zanthoxylum fagara* forest	*P. galapageium–Scalesia pedunculata–Hippomane mancinella* forest
28	Santa Cruz	*Paspalum conjugatum–Blechnum brownei* herbgrass meadow	*P. conjugatum–B. brownei* grassland
30	Santa Cruz	*Scalesia pedunculata–Zanthoxylum fagara* forest	*Scalesia pedunculata–(P. galapageium)* forest[2]
19	Santa Cruz	*Pteridium aquilinum–Jaegeria gracilis* fern meadow	*P. aquilinum–(J. gracilis)* fernland[2]
15	Santa Cruz	*Jaegeria crassa* herb–fern meadow	*Jaegeria crassa* herbfield
53	Cerro Azul, Isabela	*Pisonia floribunda–Hippomane mancinella* steppe forest transition to open forest	*(P. floribunda–H. mancinella)/Croton scouleri* scrub[2]
54	Isabela	*Centella asiatica–Paspalum conjugatum–Rhynchospora corymbosa* herb–sedge meadow	*C. asiatica–R. corymbosa* herbfield
55	Isabela	*Baccharis gnidiifolia–Scalesia cordata* steppe scrub	*[Psidium galapageium]/(B. gnidiifolia)* scrub[3]
9	Fernandina	*Bursera graveolens–Macraea laricifolia* steppe forest	*B. graveolens/M. laricifolia–Cordia revoluta* scrub
5	Fernandina	*Lippia rosmarinifolia–Polypodium tridens* shrub savanna	*[L. rosmarinifolia–Borreria ericifolia]/P. tridens* fernland[3]

[1]Species to left of backslash "/" are taller than those to the right of this sign.
[2]Names in parentheses refer to conspicuous species with canopy cover 10–19%.
[3]Names in square brackets refer to conspicuous species with canopy cover 1–9%.

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CARTOGRAFIA DE LA VEGETACION EN LAS ISLAS GALAPAGOS

Charles Huttel[1]

RESUMEN

Se describe la realización, en base a imagenes Landsat, fotografías aereas y recorridos de campo, de mapas de vegetación en las islas Galápagos; los mapas son a escala 1/50,000 en las zonas de uso agrícola y a escala 1/100,000 en las zonas de Parque Nacional. Una vez establecidas las bases cartográficas, se escogió representar la cobertura vegetal con tres niveles de información: (1) la zonación climática, (2) la fisionomía y la densidad de la vegetación y (3) algunas anotaciones de plantas dominantes. Se hace la critica del método empleado y se proponen vías para completar o continuar este primer intento de cartografía de la vegetación en el conjunto de las islas.

Para cartografiar la vegetación existen varias alternativas de acuerdo al nivel de integración al cual se quiere llegar (Ozenda, 1986). La gama va desde mapas de distribución de especies, que sólo representan una variable, presencia/ausencia de una especie, hasta mapas fitocenóticos que tratan de describir los conjuntos de plantas de una zona homogénea y sus relaciones entre ellos y los parámetros abióticos.

La elaboración de un mapa temático requiere fundamentalmente información de dos tipos; por un lado, un fondo topográfico con relieve, hidrografía, e infraestructura y, por otro, la información temática que se quiere cartografiar: información abiótica (parámetros climáticos, edafológicos . . .), biótica (vegetal o animal), o de actividades humanas.

La Cartografia de la Vegetacion en Galapagos

OBJETIVO Y ESCALA

No existía una cartografía homogénea que cubra todo el archipiélago, sólo habían croquis realizados a varias escalas, con criterios diversos, y sobre todo en la isla Santa Cruz (entre otros, Bowman, 1961; Itow & Weber, 1974; Colinvaux, 1974). La cartografía que se va a describir a continuación tiene varias imperfecciones que se analizarán, pero presenta la ventaja de haber sido realizada con los mismos criterios en todas las islas.

La finalidad de la cartografía solicitada no era muy clara. Para INGALA (Instituto Nacional de Galápagos), organismo que encargó y financió los trabajos, existía la necesidad de tener un mapa del tipo de uso del suelo en las zonas agrícolas, lo que correspondía también al deseo de PRONAREG (Programa Nacional de Regionalización Agraria) de completar tal cartografía que ha emprendido este organismo a nivel nacional. En lo que a zonas del Parque Nacional se refiere, hubo un mayor interés de parte de SPNG (Servicio del Parque Nacional Galápagos) y ECChD (Estación Científica Charles Darwin). En ambas áreas, se desprendía la necesidad de poder contar con un documento descriptivo sin mayor alcance científico.

La gama de escalas de los mapas está condicionada por la escala de los documentos de base (fotografías aéreas) y la escala definitiva fue fijada por INGALA. Se establecieron las escalas de 1/50,000 en las zonas de uso agrícola y de 1/100,000 en las zonas del Parque Nacional. Las

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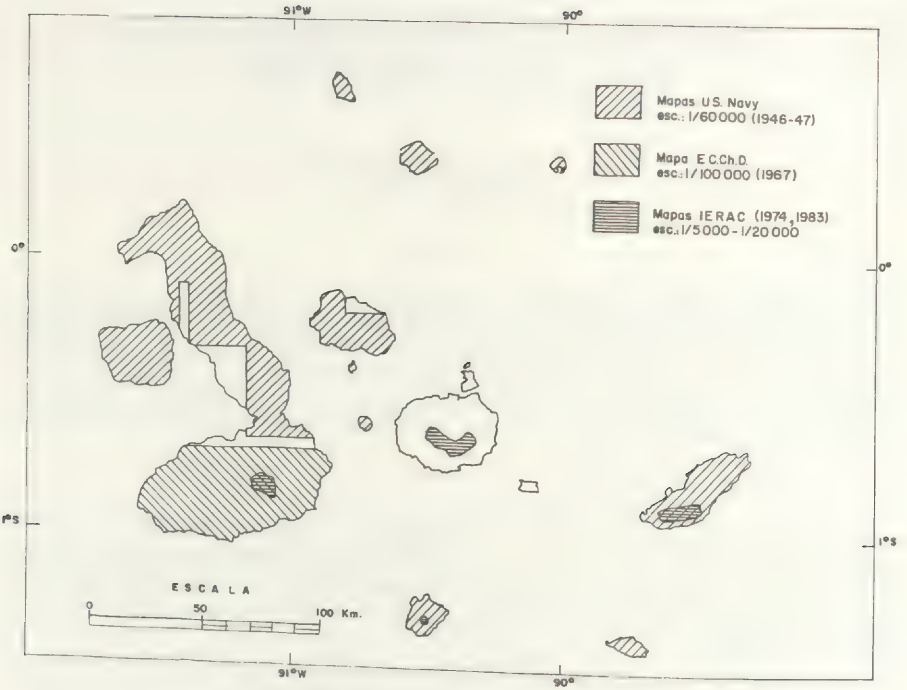

FIGURA 1. Ubicación de las zonas con información cartográfica.

fotografías aéreas no permiten, en la mayoría de los casos, pasar a una escala más grande en las zonas de uso agrícola sin cambiar totalmente los métodos de trabajo; los mapas de las zonas del Parque Nacional bien podrían reducirse a la escala de 1/200,000.

LOS DOCUMENTOS BASICOS DISPONIBLES

El primer paso en la elaboración de los mapas fue conseguir o elaborar un mapa base. Por encontrarse en proceso de realización, no existen mapas del IGM (Instituto Geográfico Militar) en la provincia insular, y la base tuvo que ser confeccionada a partir de mapas publicados en otras partes, principalmente los de U.S. Navy (ver la Figura 1 de las zonas cubiertas por mapas disponibles), de imágenes Landsat (RBV y MSS), y de fotografías aéreas. Este trabajo lo realizó el Departamento de Geomorfología de PRONAREG.

La información satelitaria (Landsat 2, 3, y 4) es fragmentaria y, revisando las imágenes disponibles desde 1979 hasta 1984, no hemos encontrado documentos utilizables para todas las islas. Por suerte, existen imágenes de buena calidad en la isla más difícil de recorrer, Isabela. La recopilación de las fotografías aéreas disponibles llevó algunas sorpresas; sorpresas gratas por la cantidad de tomas realizadas a varias fechas, sorpresas ingratas por la calidad iregular de las fotografías y por los gaps todavía existentes. Las fotografías disponibles para el público son tomas de los años 1959, 1960, 1963, 1982, y 1985; las escalas varían de 1/25,000 a 1/60,000 (Figura 2). A pesar de todas estas tomas, quedan dos zonas no cubiertas en el sur de la Isla Isabela: una en la zona de uso agrícola y otra en la vertiente oeste del Cerro Azul. Lastimosamente, todas estas fotografías no son aptas para una fotointerpretación de la vegetación; en particular las tomas de 1982 y algunas de 1985 no

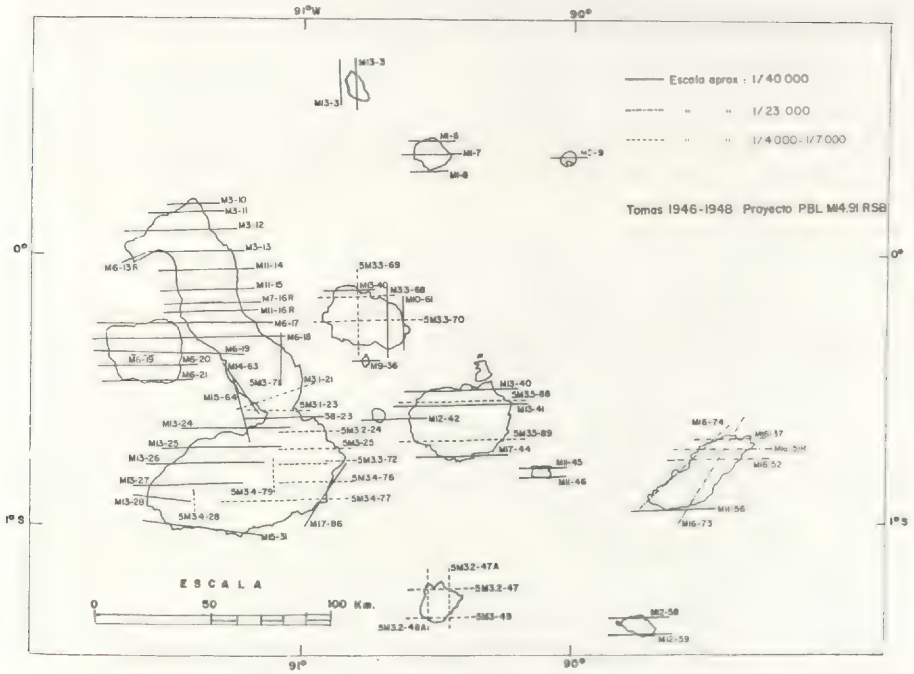

FIGURA 2. Ubicación de las líneas de vuelo de la fotografías aéreas recientes. Cada línea representada está identificada por su número precedido del número del rollo de la película.

tienen ni la nitidez ni el contraste convenientes. Las líneas de vuelo escogidas para la fotointerpretación constan en un croquis en anexo. Cabe señalar que todas las fotografías disponibles no están representadas en este croquis; existiendo líneas duplicadas en las misma zona y lineas a escalas grandes no fueron utilizadas, como las tomas del proyecto Fondeadero, por ejemplo.

Existen en el IGM juegos de fotografías antiguas (1946–1948) a escalas diversas (1/4,000–1/40,000) de las cuales no se pueden obtener copias por falta de negativos (ver Figura 3). Estas tomas son de calidad variable y permiten cubrir parte de los "gaps" de las tomas modernas. Si algunas líneas tienen la calidad suficiente para estudios de detalle, otras son tomas de baja altura y en parte borrosas. Además, las fotografías de las zonas agrícolas se encuentran demasiado desactualizadas para su empleo en una cartografía del uso actual.

En las fotografías se precisaron los limites de las zonas climáticas y se trazaron las delimitaciones de zonas homogéneas en lo que a vegetación se refiere; en pocos casos fue posible reconocer especies características.

Los trabajos de campo fueron intensivos en las zonas agrícolas y en las islas de menor tamaño. El tiempo reducido de permanencia en el campo, así como las dificultades de acceso no permitieron observar todas las unidades delimitadas en las fotografías aéreas. Por ejemplo, en las islas Isabela y Fernandina, sóla se realizaron recorridos desde la costa hasta la cumbre de cada volcán.

LA CARTOGRAFIA REALIZADA

Por el corto tiempo concedido para la realización de los mapas, la escala de la fotografías aéreas y la imposibilidad de revisar visualmente cada unidad delimitada en las fotos, se decidío elaborar

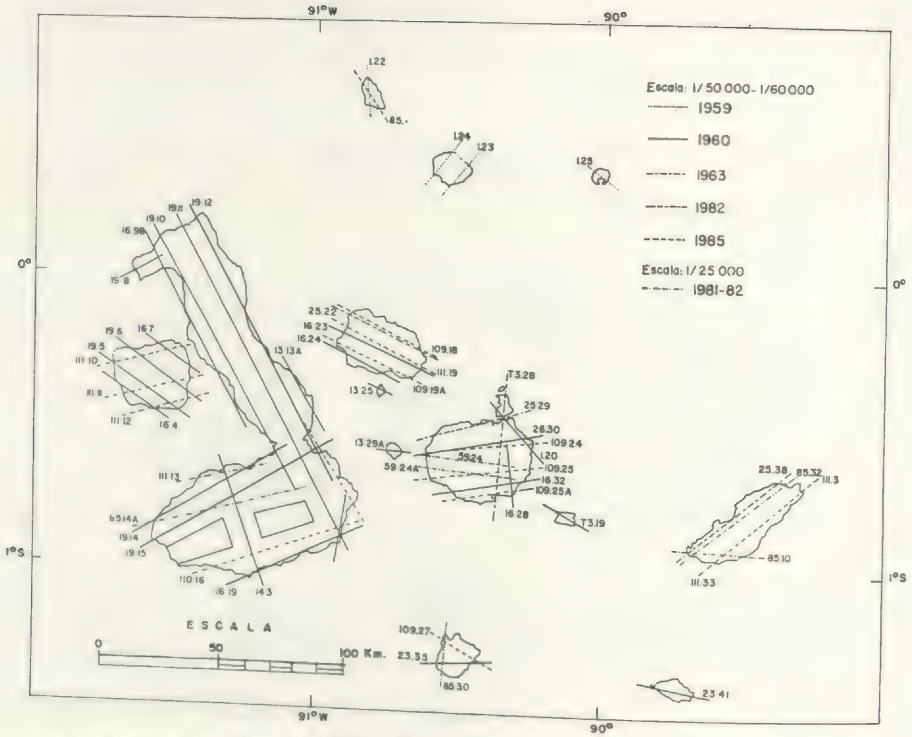

FIGURA 3. Ubicación de las líneas de vuelo de las fotografías aéreas antiguas. Cada línea representada está identificada por su número precedido del número del rollo de la película.

un mapa que represente los tipos de vegetación clasificados en formaciones vegetales diferenciadas por su fisionomía. Si tal tipo de cartografía puede ser criticada por los especialistas, presenta la ventaja de poder ser levantada rápidamente y de ser comprensible por no-especialistas. A pesar de habernos limitado a un mapa fisionómico, hemos podido integrar en su concepción tres niveles de información.

El *primer nivel* se refiere a las grandes zonas climáticas, de régimen de humedad principalmente. Las imágenes satelitarias sirvieron de base para la delimitación de estas zonas. La determinación de los regímenes climáticos, tales como fueron definidos en los trabajos cartográficos en la región costanera del Ecuador, se hizo principalmente en función del número de meses secos. Las escasas estaciones climatológicas se utilizaron para establecer la correlación entre regímen climático y tipo de vegetación, la cual permitió, finalmente, determinar las zonas climáticas en el campo. La zonificación propuesta no es la usualmente admitida para las islas Galápagos. La división en cinco zonas climáticas no solo tiene la ventaja de ser comparable con la zonificación realizada en el continente, sino que permite también homogeneizar los nombres de los diferentes pisos que hasta ahora tienen nombres basados en varias características. La denominación actual se refiere a criterios climáticos como en "zona arida," a plantas dominantes como en "zona a *Scalesia*" o "zona a *Miconia*" (además estas plantas no estan presentes en todas las islas) a un color como en "brown zone" o finalmente a características indefinidas como en "zona de transición." La excelente correlación existente entre zonas climáticas y formaciones vegetales justificó plenamente la inclusión de un parámetro abiótico en un mapa de vegetación y la adopción de esta nueva zonificación. Este primer nivel dió resultados confiables en toda la zona cartografiada.

El *segundo nivel* se refiere a la fisionomía de la vegetación. Los trabajos a este nivel encontraron sus limitaciones en la escala y la calidad de las fotografías aéreas y en el recorrido parcial de campo. Si no existe ningún problema para identificar en las fotografías aéreas las formaciones arbóreas o árboles aislados, no es el caso de las formaciones arbustivas ni de las formaciones herbáceas. Las formaciones arbustivas forman, en las fotografías a 1/60,000, un velo de granulación muy fina y las formaciones herbáceas se distinguen par la ausencia de granulación. A este criterio fisionómico cualitativo se pudo añadir un criterio cuantitativo, estimando la densidad de la cobertura vegetal expresada en cuatro grados: cobertura cerrada, abierta, muy abierta, y no significativa. También fue posible representar unidades complejas donde las asociaciones entre varias fisionomías fueron reducidas a combinaciones de dos formaciones, favoreciendo sistemáticamente la vegetación leñosa.

Los resultados correspondientes a este segundo nivel pueden ser criticables en dos aspectos. Las delimitaciones de zonas homogéneas en las fotografías son confiables en los casos de contacto de dos zonas muy contrastadas, como ocurre con una colada de lava y los terrenos circundantes; en el caso de variaciones progresivas de las características observadas en las fotografías, la ubicación del limite es, obviamente, arbitraria lo que traduce muy bien el término de foto*interpretación*. La segunda fuente potencial de errores es la identificación en los clichés de la fisionomía de la vegetación, siendo las formaciones arbustivas y herbáceas más sujetas a tales errores que las formaciones arbóreas. Es obvio que las limitadas comprobaciones de campo no permitieron corregir todos los errores de fotointerpretación.

El objetivo del *tercer nivel* solo se pudo cumplir de manera parcial; la meta era proporcionar alguna información de tipo florístico. En las fotografías es posible distinguir facilmente, gracias a la tonalidad y al grano, los bosques de *Bursera*, de *Sapindus*, y los manglares, pero fue imposible diferenciar un bosque de *Scalesia* de un bosque de *Zanthoxylum*, por ejemplo. Estas dificultades son insuperables en las formaciones arbustivas. Por esta razón, la información florística no puede ser extraída directamente de las fotografías y sólo se han indicado las especies características o dominantes encontradas a lo largo de los recorridos de campo.

Posibles Evoluciones de esta Cartografia

Los documentos realizados en el marco del convenio INGALA-PRONAREG constituyen el primer intento de una cartografía de la vegetación del archipiélago. Por el reducido tiempo de los trabajos de campo y las dificuldades de acceso a muchos sitios, estos mapas no pretenden ser documentos definitivos. Por la metodología empleada se puede admitir que los límites propuestos en los mapas son confiables, pero que la identificación de algunas unidades cartográficas es dudosa.

Por tal razón, una paulatina revisión del contenido de las unidades cartografiadas sería conveniente y podría hacerse de dos maneras complementarias: primero, recogiendo la información de personas que han visitado zonas donde no se efectuaron recorridos de campo y traduciendo esta información en los terminos previstos por la leyenda la que, por suerte, es abierta y permite combinaciones. La segunda manera sería conseguir información nueva en las zonas poco conocidas.

Evoluciones más interesantes se refieren a una reformulación de la información sobre las formaciones vegetales. Esto implica un cambio radical de la leyenda para que se acerce más a metas científicas clásicas. En efecto, la leyenda actual tiene un nivel descriptivo muy bajo por las razones expuestas anteriormente.

Según los objetivos propuestos podemos sugerir dos vías diferentes. La primera se refiere a un perfeccionamiento del mapa fisionómico. Una descripción fisionómica clásica de las formaciones vegetales podría utilizar la clasificación internacional elaborada por la UNESCO (1973) que señala 255 tipos de formaciones vegetales y que incluso propone una gama de colores para su representación cartográfica. Si esta clasificación es muy facilmente aplicable en las formaciones de bosque no ocurre igual en las formaciones arbóreas abiertas, en las formaciones arbustivas, ni en las

herbáceas, particularmente cuando se encuentran asociadas, como es a menudo el caso en Galápagos. No existen suficientes datos para opinar sobre la conveniencia de la aplicación de la clasificación UNESCO en Galápagos, pero sí se puede anticipar que tal cartografía requeriría un amplio trabajo de campo ya que sólo pocos sitios se encuentran actualmente descritos con la precisión necesaria. También se puede temer que las definiciones de las formaciones conducirían a la reunificación de varias de nuestras unidades y a un consecuente empobrecimiento de la información. Por fin, una descripción fisionómica conformaría un documento descriptivo de grán valor para los usarios de los mapas, pero no permitiría una evolución hacia trabajos más analíticos.

La cartografía de unidades definidas por su composición florística parece una vía potencialmente más excitante para los científicos, pero supone un largo trabajo de campo. Los logros de una investigación no justificarían una cartografía exhaustiva de todas las islas ya que los resultados esperados pueden lograrse en base a investigaciones en zonas previamente escogidas. La relativa pobreza florística de Galápagos y la existencia de condiciones ecológicas bien contrastadas son un aliciente para un trabajo de este tipo. Cabe indicar que estudios de esta naturaleza no serían nada nuevo en el contexto de Galápagos (Hamann, 1981) pero la representación cartográfica de los resultados sí sería novedosa.

La base para estos trabajos sería la definición de conjuntos florísticos, ya sea por el método de las asociaciones vegetales (escuela de Zurich-Montpellier) o por el método de los grupos ecológicos (Duvigneaud). Es probable que este último método sea el más adaptado para el estudio de formaciones no climácicas, formaciones frecuentes en el archipiélago y que presentan un gran interés. El ordenamiento de los levantamientos de campo y de los grupos ecológicos identificados permitiría una amplia diversificación de las conclusiones.

En primer lugar sería posible determinar con mayor precisión los conjuntos florísticos característicos de las varias zonas climáticas. Hasta ahora existen listas de plantas encontradas en varios pisos, pero la caracterización debería realizarse mediante la presencia (o la ausencia) de grupos ecológicos de plantas. Tal análisis de la vegetación permitiría también evaluar el carácter discriminatorio de las plantas más abundantes. Al mismo tiempo sería factible determinar de manera objetiva el número de pisos de vegetación, variable de acuerdo a los autores.

Levantamientos florísticos de las formaciones vegetales proveerían también datos para el análisis dinámico de la vegetación con por lo menos dos enfoques importantes para Galápagos: la antropización de la vegetación y el proceso de colonización de los terrenos de origen más reciente. Si varios trabajos, incluso con croquis cartográficos, se dedicaron al seguimiento de las plantas introducidas, todavía no se ha emprendido un estudio orientado hacia la dinámica de la vegetación pionera y de su evolución en las islas.

Tales investigaciones fueron iniciadas por varios autores, pero sin la componente cartográfica. Una cartografía permite no sólo localizar un objeto, sinó también ubicarlo en un conjunto más amplio. Representar sobre mapas, aunque sean éstos parciales, las formaciones vegetales descritas en base a grupos ecológicos ilustraría las interrelaciones entre los principales factores determinantes de la repartición de las formaciones vegetales en Galápagos: el clima, la edad del substrato, y la acción del hombre.

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A TWO-YEAR STUDY OF POST-FIRE VEGETATION DYNAMICS ON SOUTHERN ISABELA, GALAPAGOS ISLANDS, ECUADOR[1]

J. Bosco Nowak[2], Jonas E. Lawesson[3], Henning Adsersen[4] and Tjitte de Vries[5]

ABSTRACT

The succession and dynamics of the vegetation after the 1985 brush fire in a 200-km^2 area at the southern flanks of Sierra Negra volcano, Isabela, Galápagos Islands, were studied during two years by means of survival counts and permanent study plots. The study shows that some endemic and rare taxa had very little or no regeneration, whereas introduced species showed high degrees of survival and regeneration. The treeless grass vegetation seemed able to recover within two or three years, whereas the fern-dominated meadows regenerated slowly.

For over a century humans have been modifying the ecosystems of the Galápagos Islands: after colonization, many forest-covered areas were transformed into pastures, cropfields, and fruit tree plantations. Alien plants and animals were brought to the islands and some escaped. This had a profound impact on the natural vegetation in some areas (see Lawesson, this volume, for references).

Fire has always been a natural factor in Galápagos, given the presence of volcanoes. The frequent eruptions must have caused fires, as it was observed by one of the authors in 1988 on Volcán Fernandina, where several areas at the top burnt. Man-made fires have occurred during this century in colonized and uncolonized areas. On Santa Cruz, fires burnt in the highlands in 1934, 1946, 1947, 1959, 1965, and 1967 (de Vries, 1970; Eckhardt, 1972; Kastdalen, 1982; J. de Roy and Y. Carvajal, pers. comm.). Since the initiation of human colonization on the island, the impenetrable thick vegetation of the summit has been subject to great changes due to fires (Howell, 1942). Around Media Luna, a carpet of ferns 1.5–2 meters thick, lichens, and organic litter have been destroyed, leaving only a few centimeters of soil (de Vries, pers. obs.). On Isabela, Volcán Alcedo was ravaged by fire in the highlands in 1970 (Hamann, 1975).

The fires generally change the floristic composition into communities dominated by herbs and shrubs, whereas trees suffer due to their slower regeneration. The lack of trees and shrubs in the highlands of the populated islands may in part be the result of frequent fire. However, long-term monitoring should be undertaken to prove this theory. The great fire on the southern flank of Volcán Sierra Negra on Isabela in early 1985 was a sad event, but it presented a unique opportunity for initiating studies on fire ecology in the Galápagos. A multidisciplinary approach was set up by the

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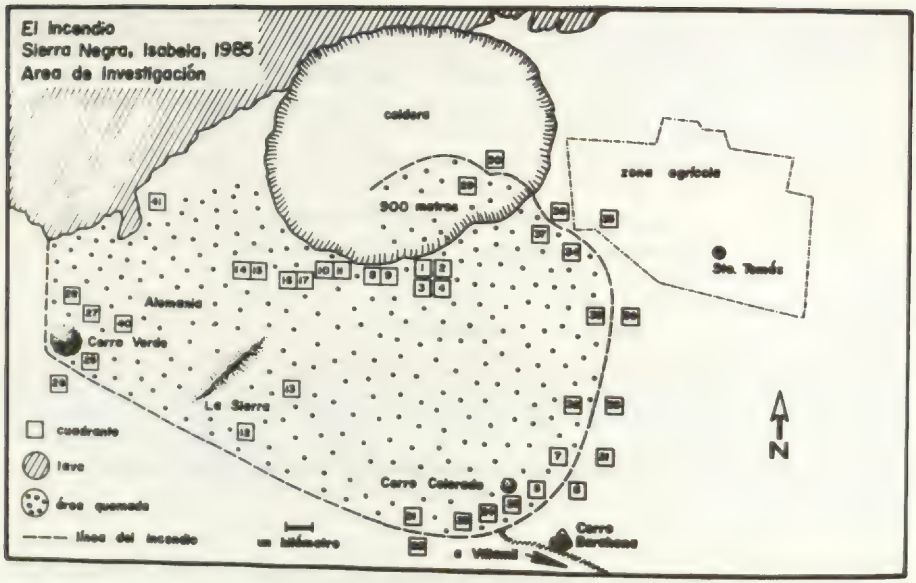

FIGURE 1. Map of study area. Numbers refer to quadrats.

Charles Darwin Research Station, The Galápagos National Park Service, and research institutions, involving zoologists, botanists, geographers, and others (see Adsersen, 1985; Anonymous, 1985a, b). A group of researchers from the home institutions of the authors initiated the vegetation succession studies. This paper deals with the background of the fire, the area and its characteristics, the preliminary results on tree survival, and the general vegetation succession observed in the treeless pampa region.

THE STUDY AREA

The burnt area is situated on the southern flanks of the 1,100-m-high Volcán Sierra Negra, Isabela Island (Fig. 1). Since the settlement of the villages of Villamil and Santo Tomas in 1893, the area has been affected by introduced cattle, goats, donkeys, and horses. Alien plants were introduced long ago, and some spread rapidly, especially *Psidium guajava*, the common guava (Lawesson & Ortiz, this volume). A relatively large area around Santo Tomas on the southeastern flanks was cleared for agricultural purposes, and different types of crops were cultivated there.

The area is therefore not pristine, but rather is a strongly influenced landscape; however, some parts have high conservation interest. Despite the rather easy access to the area, it has been poorly investigated botanically. A brief account of the vegetation was given by Hamann (1981), and a report based on transects was given by Adsersen (1985) after a visit there during the fire. A number of endemic and rare plants occur in the area and are vulnerable to disturbance. The vegetation types and their distributions thus result from natural and human-induced factors (Hamann, 1981). The most significant vegetation types to be distinguished in the area are the following:

Semideciduous forest (80–250 m). This forest has a canopy stratification in different levels and is dominated by the trees *Pisonia, Croton, Sapindus, Zanthoxylum*, and others. There are well-marked seasonal changes; the trees tend to shed their leaves during the cool season, and the herbs are mainly seasonal. The fuel load (i.e., the available amount of easily burnable organic matter) in this vegetation type is generally low and restricted to the short periods with precipitation.

Closed evergreen forest (250–500 m). This is a low forest in large areas mainly dominated by the introduced guava (*Psidium guajava*), but in smaller areas with original vegetation typical dominants are *Zanthoxylum fagara, Tournefortia* spp., *Psidium galapageium, Solanum erianthum, Cordia leucophlyctis, Croton scouleri,* and others. Locally, *Scalesia cordata, Acnistus ellipticus,* and *Trema micrantha* are common. The abundance of terrestrial and epiphytic ferns is characteristic. When its original composition is maintained, the fuel load is moderate, and the fire potential is limited by the humidity. However, when *P. guajava* invades, an increased fuel load and dryness have been observed, at least in the westernmost part of the area, dominated by cinder soils.

Open evergreen forest and scrub (500–800 m). This vegetation type forms a floristic and physiognomic transition to the treeless pampa vegetation, which is found at higher altitudes. The most common arboreal is *Psidium guajava,* but individuals of *Zanthoxylum, Acnistus, Tournefortia,* and *Darwiniothamnus* occur locally. They develop a shrubby habit with increasing altitude. Due to the invasion by alien trees and grasses, the fuel load of this vegetation is probably larger than the original vegetation, making an eventual fire more destructive.

Pampa (800–1,100 m). The treeless vegetation may be divided into two major types:

1. A native fern vegetation, which is presently restricted to inclined and irregular terrain and dominated by *Pteridium aquilinum, Cyathea weatherbyana,* and others. This type of pampa is able to maintain the soil surface covered and remains humid even through long droughts.
2. A secondary grassland on flat areas with deeper soils, dominated by grasses and sedges. There is an abundance of fine fuel load, which dries out rapidly. Grasses will dry out to a flammable condition much faster than the fern vegetation.

The Fire on Isabela, 1985

The climatic conditions determined the extension of the fire. The Niño year 1983, with its extremely high precipitation, caused an immense biomass production and hence fuel load. The subsequent extreme drought of 1984–1985 dried the vegetation and the soil (Adsersen & Lawesson, 1985). The fire, most likely of antropogenic origin (Huttel & Winckell, 1985; UNEP, 1985), started in the high pampa area (Tupiza, pers. comm.) in early March and spread rapidly into a very large area. After several months of control efforts, it was finally stopped by a fire-break line from the east to the west. Its advance was stopped naturally in the northern parts by open vegetation, and inside the caldera floor with pick and shovel (Adsersen & Lawesson, 1985).

The fire was extinguished in July 1985. The extent of the fire on Isabela seems to be unmatched in Galápagos with respect to affected area (200 km^2), number of vegetation zones affected, and damage to vegetation and soil. The fire characteristics varied depending on the fuel load, i.e., vegetation, organic litter, and soil consistency, from open torching flames of rapid propagation to surface and subsurface combustion of very slow propagation (Huttel & Winckell, 1985). The impact on the vegetation was very variable, leaving some areas virtually undamaged, in others causing a complete burning of the biomass and soil.

Methods

Vegetation analysis

Forty-nine permanent quadrats (PQ) were established in July–November 1985 (Fig. 1), the majority in pairs with one in burnt and the other in unburnt vegetation, and they were visited every second or third month after the fire. The quadrats were generally 10 × 10 m, but in some

herbaceous vegetation were 5 × 5 m. In each quadrat species composition was recorded. The vegetation structure was classified according to Fosberg (1967) and Hamann (1981). Recorded for each species were cover estimated at a percentage scale and frequency by means of 10 circular samples of 0.5 m^2 taken at random inside the quadrat. Soil samples were collected in all quadrats throughout the time of study. Relative cover and frequency values were found, and an importance value was calculated as the sum of relative cover and relative frequency divided by 2.

It is outside the scope of the present paper to give a full account on the detailed investigations, but some trends have become obvious.

TREE SURVIVAL COUNTS

Trees were counted in burnt forest areas. Around selected points, the nearest 50 trees higher than 2 m were inspected and classified for (a) species identity, and (b) survival state. Survival state was classified according to three categories: NS = No Survival (completely dead); PS = Partial Survival (canopy dead, basal shoots present); and CS = Complete Survival (canopy alive).

A Relative Survival Value (SV) was defined, based on percentages of Complete Survival (CS) and Partial Survival (PS). (The Partial Survival is divided by 2 and added to Complete Survival.)

Results

FOREST ZONES

Semideciduous forest. The fire allowed relatively high survival of the tree canopy in most areas (with the exception of certain completely burnt areas), but the understory composed of *Zanthoxylum fagara, Tournefortia* species, and *Croton scouleri* was impacted severely. The three species of *Tournefortia* were found to germinate rapidly, while *Psidium galapageium* did not germinate and only rarely resprouted successfully. Successful regeneration of *Zanthoxylum fagara* and *Sapindus saponaria* was low. However, due to the high canopy survival and understory regeneration, most burnt areas seemed to have recovered their general appearance two years after the fire.

Closed evergreen forest. Approximately 90% of the *Psidium guajava* trees were canopy-killed, but around 65% resprouted. Apparently *P. guajava* can recover to its earlier dominance (Fig. 2). *Scalesia cordata* (Fig. 3), with its soft wood, was entirely killed by the fire but germinated rapidly and grew from seeds that possibly are fire- and drought-stimulated. Yet later invertebrate plagues killed or inhibited regrowth severely (Fig. 4). *Trema micrantha,* another easily fire-killed species with soft wood, was sparsely distributed below 350 m before the fire. Those areas were rapidly taken over by *T. micrantha* after the fire, and areas previously without it were also invaded to some extent. *Solanum erianthum* seemed to benefit from the fire, reaching high importance in places. Other trees or shrubs from this zone with low regeneration within two years were *Zanthoxylum fagara, Acnistus ellipticus,* and *Darwiniothamnus lancifolius. Psychotria rufipes* and *Chiococca alba,* on the other hand, seemed to have no regeneration at all.

Open evergreen forest and scrub. Due to accumulations of dry fern fronds, this zone burnt intensively, and almost all trees were top-killed. Regeneration of the dominant tree species *Psidium guajava* by resprouts seemed effective, while the native species *Zanthoxylum fagara* and *Tournefortia rufo-sericea* regenerated slowly from seed.

FIGURE 2. Burnt *Psidium guajava* forest, November 1985.

FIGURE 3. Young saplings of *Scalesia cordata* colonizing parts of the fire-break line, November 1985.

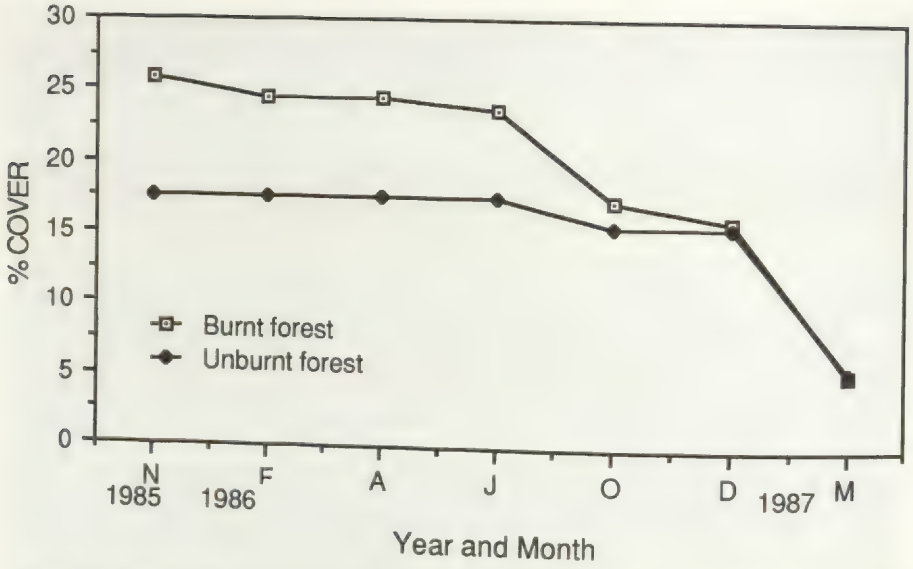

FIGURE 4. Percent cover of the declining *Scalesia cordata* in burnt and unburnt vegetation, average values from seven burnt and two unburnt quadrats.

TREE SURVIVAL COUNTS

The figures for tree survival are given in Table 1. Apparently the capacity to resprout with basal shoots (PS) is species specific and correlated with a low canopy survival (CS). The species with the highest canopy survival—*Hippomane mancinella, Pisonia floribunda,* and *Croton scouleri*—do not resprout. Species with lowest Survival Value, *Trema micrantha* and *Tournefortia* species, seemed to have a high regeneration capacity by means of seeds. *Zanthoxylum fagara* with low Survival Value showed remarkable regeneration at low elevations. The response of *Psidium guajava* (PS > NS > CS) to fire is similar to the also introduced *Eugenia jambos* and the endemic *Psidium galapageium,* all in the Myrtaceae. Similar observations on *Eucalyptus globulus* and *Melaleuca quinquinervia* (Wade et al., 1980) suggest a common trend for basal sprouting within this family.

The successful establishment after two years followed this sequence: *Trema micrantha* > *Tournefortia* species > *Solanum erianthum* > *Scalesia cordata* > *Zanthoxylum fagara* > *Acnistus ellipticus* > *Sapindus saponaria*. The low density of *Trema micrantha* in unaffected *Psidium guajava* forest contrasts with its high regeneration and dominance in burnt areas. The presently *T. micrantha*-dominated forests may eventually be replaced by *Psidium guajava*. Several dead individuals of *T. micrantha* observed in the unaffected vegetation support this.

Hendrix & Smith (1986) reported on survival and ability of basal resprouting of shrubs on the rim of Fernandina after the 1968 eruption. They found a rapid recovery of *Solanum erianthum* by seeds and to a lesser extent by sprouting from buried parts. *Scalesia microcephala,* a close relative of *S. cordata,* recovered well, but more slowly and only from seeds. *Zanthoxylum fagara* seemed to reimmigrate very slowly by means of seeds. This agrees with our findings, but the observation of very fast resprouting for *Tournefortia rufo-sericea* differs from our experience on Sierra Negra. This may be due to different disturbance of the original vegetation: on Fernandina the vegetation was covered by tephra, but no fire was recorded, whereas the deeply penetrating fire on Sierra Negra may have destroyed too much of the underground organs for survival of *Tournefortia*.

For conservation purposes it is important to identify which species or species groups (endemic,

TABLE 1. Tree survival; survival proportion, survival states, and survival values for 11 species.

	Numbers of trees	Survival proportions	CS% Complete Survival	PS% Partial Survival	SV% Survival Value (= CS% + ½ PS%)
Pisonia floribunda	52	CS > NS	52	0	52
Hippomane mancinella	63	CS > NS	52	0	52
Croton scouleri	27	NS > CS	48	0	48
Psidium guajava	182	PS > NS > CS	12	64	44
Psidium galapageium	173	PS > NS > CS	18	45	40.5
Eugenia jambos	54	PS > NS > CS	9	28	37
Sapindus saponaria	47	NS > CS > PS	30	9	34.5
Acnistus ellipticus	7	PS > NS	29	0	29
Zanthoxylum fagara	232	NS > CS > PS	22	4	24
Tournefortia species	32	NS > CS	25	0	25
Trema micrantha	19	NS	0	0	0

TABLE 2. Post-fire regeneration. Species numbers, percentages, and origins (first two years following fire). The column with "Otherwise" indicates the number of species that could not be ascribed to one of the categories during the study.

	Total		No Regeneration		Slow Regeneration		Highly favored		Otherwise	
	Species	%	Species	%	Species	%	Species	%	Species	%
Total	208	100	28	13.5	34	16.3	68	32.7	78	37.5
Endemic	40	19.2	9	22.5	9	22.5	8	20.0	14	35.0
Native	139	66.8	19	13.7	25	18.0	44	31.6	51	36.7
Introduced	29	13.9	—	—	—	—	16	55.2	13	44.8

native, or introduced) have suffered significant changes in abundance due to the fire. As seen in Table 2, endemic species are strongly represented in the categories of no or slow regeneration. Introduced species, if significantly affected by the fire, are among the highly fire-favored species.

Grassland pampa. The grasslands in the pampa zone are restricted to plains with deep soils. Part of their total area was burnt by deep, slowly advancing fires. Burnt parts without conspicuous survival were selected to follow recolonization and succession, which depended almost entirely on immigration. For completely burnt grasslands, a model of five successional phases is appropriate.

1) Bryophytic phase. In periods of prolonged humidity, a delicate cover of mosses (e.g., *Funaria hygrometrica*), hepatics (e.g., *Marchantia* species), and plantlets of *Pteridium aquilinum* is formed on the loose ash or gravel soil. Rhizomes of *Equisetum bogotense* survived the fire, and hence this species was abundant during this phase (Fig. 5). In times of drought this vegetation disappears completely. As shown in Figure 6, *Funaria hygrometrica* dominates the vegetation for more than a half year.

2) Phase of spaced seasonal herbs. Seasonal herbs, such as *Sonchus oleraceus, Gnaphalium purpureum, Lobelia* ×*alapensis, Conyza canadensis,* and others are the first vascular pioneer plants. They established themselves well spaced in the bryophytic carpet and did not gain high

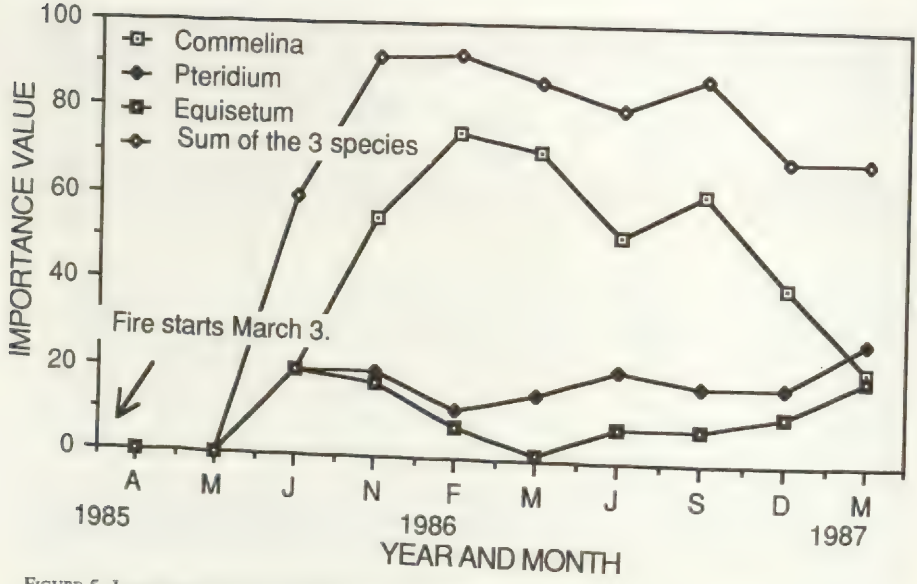

FIGURE 5. Importance values in percent, burnt fern-meadow, quadrat 8.

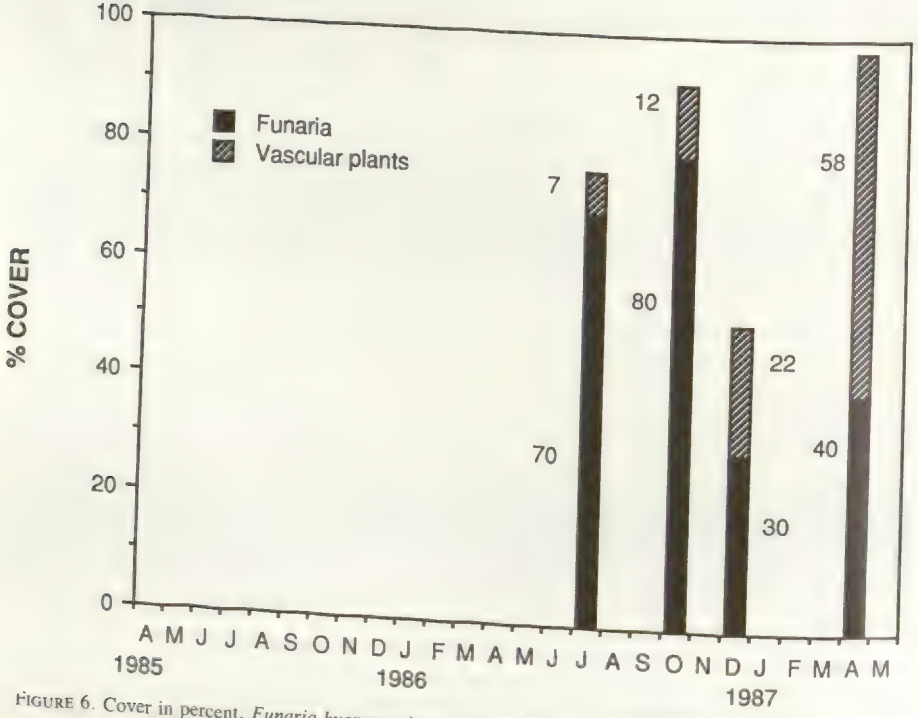

FIGURE 6. Cover in percent, *Funaria hygrometrica* compared to other plants, quadrat 2b.

FIGURE 7. *Pteridium aquilinum* and *Commelina diffusa* are among the first plants to reestablish newly burnt pampa vegetation.

coverage. Characteristic for many such species (except *L.* ×*alapensis*) is a high capacity for wind dispersal and a short life cycle.

3) Phase of Commelina diffusa. This species may arrive with the first pioneers. It is dispersed by seeds or more frequently by transport of asexual parts. With its creeping concentric growth, few individuals may cover large areas (Fig. 7). Figure 8 demonstrates the cover increase of *C. diffusa* in one PQ: in February 1986 it covered 1%; by December of the same year the cover was 60%. Caused by the abundant precipitation in May 1987, *C. diffusa* had almost disappeared completely. We ascribe this to competition from other plants. Importance values in Figure 9 show succession before and after the Phase of *C. diffusa: Equisetum bogotense* survived the fire, gained shortly afterwards high importance, but was replaced one year after the fire by *Commelina diffusa*. Less than one year later grasses rose to dominance.

4) Phase of meadow establishment. In the formation of grass meadows, grasses, sedges, and other members of grass communities (e.g., *Cyperus brevifolius, Centella asiatica,* and others) increase in importance. During this phase the vegetation seems to reach its highest diversity. Figure 10 shows the diversity in a burnt PQ to be twice as high as in the control PQ; most of the species of the unburnt community are already present in the burnt area (9 of 12 species).

5) Phase of mature meadow. Once the species of the original meadow communities have passed a cover sum of 100%, the pioneer species seem to be eliminated by interspecific competition, and the diversity approaches that observed in unburnt areas (Fig. 11).

The speed of the described succession in the pampa zone is highly variable as shown by the three PQs represented here. In PQ INV 2 colonization started after 15 months, whereas PQ 11 has reached the meadow establishment phase within the same time. PQ 15 seems to be representative for the burnt meadows: Within three to seven months after the fire, colonization started; after one year the

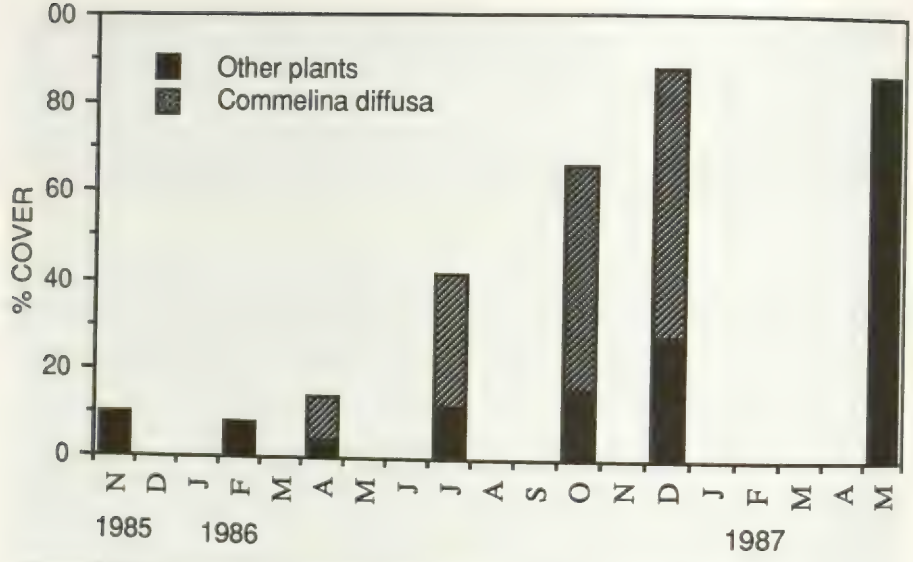

FIGURE 8. Cover in percent for *Commelina diffusa* compared to other plants, quadrat 15.

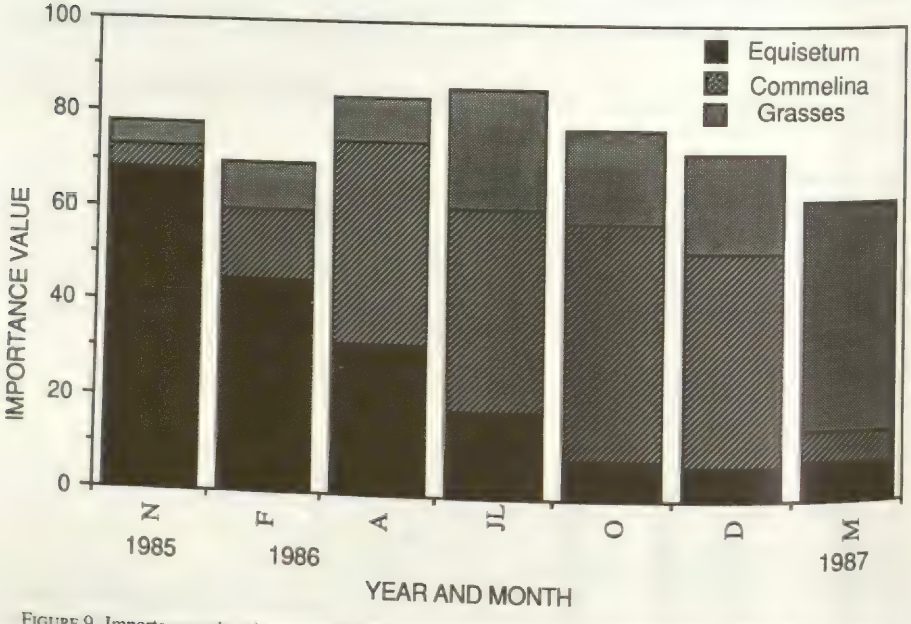

FIGURE 9. Importance values in percent for *Equisetum bogotense*, *Commelina diffusa* and grass species, burnt grass-meadow, quadrat 15.

seasonal herbs phase had ended, and *Commelina diffusa* started to dominate. After approximately two years, the succession had reached the meadow establishment phase. Estimated on the basis of these tendencies, the majority of the burnt meadows will probably need approximately three years

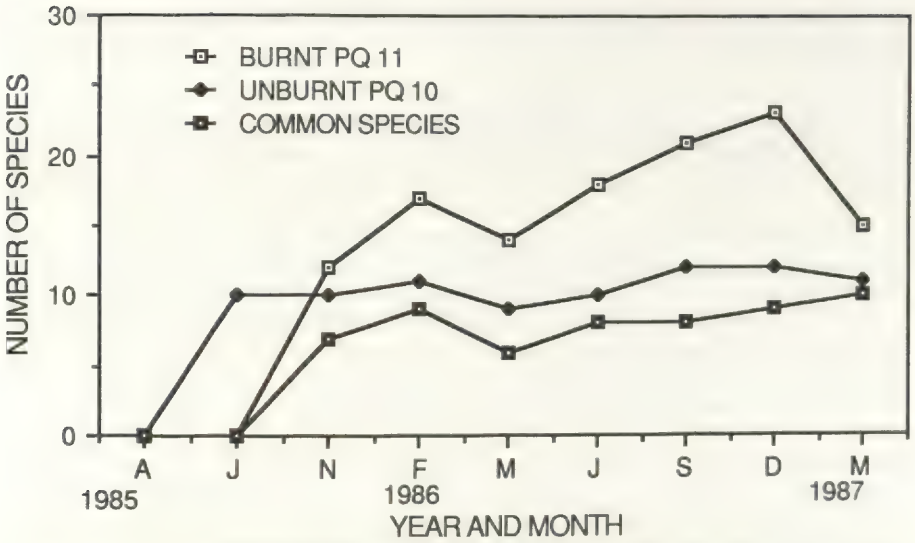

FIGURE 10. Number of species for burnt (quadrat 11) and unburnt (quadrat 10) grass-meadow, and number of species common to both.

FIGURE 11. Pampa revegetation at the rim area, November 1986.

to reestablish their former vegetation types, although with significant quantitative differences in species composition.

Fern pampa. The fern-dominated vegetation in the pampa zone, being restricted to inclined and irregular terrain, burnt intensively and almost totally, leaving only parts inside the caldera and smaller refuges intact or less affected. The lack of nonburnt control areas presents a problem, although the species composition is well known. All PQs established had a certain survival of *Pteridium aquilinum* and *Equisetum bogotense*. However, if the survival was relatively low, as was the case in severely burnt areas, a well-defined phase of *Commelina diffusa* preceded the dominance of *Pteridium aquilinum*. In less intensively burnt areas, the high survival of *P. aquilinum* produced a rapid and complete cover of vegetation, which did not permit any other plants to dominate.

In the fern pampa, pteridophytes make up the dominant and most diverse group. Only a few species showed regeneration within two years. No reestablishment of ligneous species, such as *Pernettya howellii, Darwiniothamnus lancifolius, Zanthoxylum fagara, Tournefortia pubescens,* or *Cyathea weatherbyana* was observed within the first two years.

Discussion

Even if forest originally may have dominated the high and humid flanks of Sierra Negra, fern pampa is probably one of the original vegetation types. The extensive grasslands are more likely a result of the impact of introduced herbivores than of natural tortoise grazing, which probably would produce savannalike vegetation. In the fern pampa, reestablishment of the diversity of the prefire vegetation will take a long time, probably more than ten times as long as in the grasslands, especially because the ligneous element seems to be disadvantaged. Due to the intense climatic fluctuations, the original woodlands of the high altitudes were most vulnerable to burning and further destruction by introduced herbivores, thus permitting the extensive formation of grasslands. The recent invasion by *Psidium guajava* into these areas might represent a forest reestablishment by an introduced species.

Conclusion

The preliminary results after two years of study indicate that recolonization of the burnt area is under way, and that the major vegetation types, such as forest, scrub, and meadow, are being reestablished. In the forest zones, typical pioneer species like *Trema micrantha, Solanum erianthum, Tournefortia* species, and *Scalesia cordata* dominated initially; large areas later were taken over by introduced trees, most notably *Psidium guajava*. In the higher treeless parts of the study area, secondary grass meadows have been reestablished after initial phases dominated by *Commelina*. The fern pampa and thickets, which probably represent a more natural type, with *Cyathea* and *Pteridium*, however, are only very slowly recovering their composition and structure, and in some parts they are being taken over by grasses. Through successfully resprouting and germinating, the alien plants, especially grasses, recover rapidly after the initial setback and fill in the spaces left by the more slowly recovering natives. A large part of the native and seed bank has been destroyed by the fire, making the vegetation more vulnerable to subsequent fires.

When alien grasses and trees invade the native vegetation, the fuel load is increased, possibly allowing hotter and more destructive fires. They also provide a continuous fuel on the ground, which dries quickly and allows fires to be carried faster and farther. This is especially the case in the scrub and fern-rich vegetation above 800 m, which now is taken over by grasses and sedges. The original vegetation kept the moisture high on the shaded soil surface, and the high coverage inhibits grasses or herbs. But due to the continuous grazing and degradation during this century, this

area has been turned into grass-dominated meadows. This is probably the reason why these areas burnt so intensively. Similar cases have been reported from Hawaii (Smith & Tunison, in press).

The use of fire to favor native species or vegetation types is well known from continental ecosystems and has been suggested in Galápagos for control of alien plant species (Loung, 1987). However, the experiences from this study indicate that fire cannot be considered as a useful tool to control alien species and promote natives in Galápagos, except in some very special cases. The possibility of prescribing fires in limited areas for specific purposes, combined with additional management measures, should be carefully investigated and evaluated. A continuation of the study on Isabela is therefore of highest importance. In subsequent papers we will report the development of important soil factors (N-content, C-content) in the post-fire succession. The results of the on-ground recording of successional stages will be followed up by estimations of their spatial extension by means of satellite images (cf. Meyer & Adsersen, this volume).

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THE DYNAMICS OF *SCALESIA CORDATA* (ASTERACEAE) IN DIFFERENT HABITATS IN SIERRA NEGRA, ISABELA, GALAPAGOS[1]

Tjitte de Vries[2] and Arnaldo Tupiza[3]

ABSTRACT

Scalesia cordata Stewart was studied in six permanent quadrats of 10 × 10 m (5 plots) and 20 × 20 m (1 plot) on the southern and eastern flanks of the Volcano Sierra Negra, Isabela Island. The stands were in different stages of maturity when the quadrats were established, presenting marked differences in separate life classes. Emergence of seedlings was not synchronized over the same years, but 1973 and 1985 were producing many seedlings. The age of some trees was exactly known, others were calculated and extrapolated based on growth rates. Trees in dry habitats grew slower and reached older ages than those in humid habitats. All plots suffered from extreme conditions with heavy rains in 1982–1983 or severe drought in 1984–1985; mortality varied among quadrats. Drought, and not the rains, marked years of new growth in humid habitats, contrasting with dry habitats where no new plants grew in 1982–1985. In the drier part of the habitat (site 5) the oldest tree was calculated to be 65 years old when it died. In the more humid parts most die in their first five years, a few live 20–40 years and some survive longer. Some trees flower for the first time after 40 months. Most trees had flowers in April, but in 1978 a season prolonged up to October was observed.

The endemic genus *Scalesia* Arn. (Asteraceae) is widespread in the Galápagos Archipelago. Most species are found in the arid regions of the islands (Eliasson, 1974; Hamann & Wium-Andersen, 1986).

Scalesia pedunculata Hook. f. is found in the humid highlands of Santa Cruz, San Cristóbal, Floreana, and Santiago; whereas *Scalesia cordata* is restricted to humid and semiarid regions of Sierra Negra and Cerro Azul of Isabela.

Scalesia microcephala Robins. is found in humid and arid regions of the volcanoes Alcedo, Darwin, Wolf, Ecuador (Isabela), and Fernandina. On Santa Cruz, *Scalesia pedunculata* is restricted to the humid highlands, whereas *S. affinis* Hook. f., *S. helleri* Robins., *S. aspera* Anderss., *S. crockeri* Howell, and *S. incisa* Hook. f. are found in the arid lowlands in contrast with the situation on Sierra Negra, where *S. cordata* and *S. affinis* meet at lower middle altitudes.

This situation prompted us in 1974 to establish permanent plots of 10 × 10 m and 20 × 20 m in six different habitats to follow the growth rate and phenology of *Scalesia cordata*. The quadrats were checked twice a year (in the warm season in April and the cool season in October). In this paper the resulting data on the dynamics, different life classes, and growth rates of *Scalesia cordata* are presented. Two plots (sites 2 and 3) were seriously affected by extensive fires in April–June 1985, interfering with the project but providing additional data.

[1]This long-term project was supported by the Charles Darwin Research Station and the Galápagos National Park Service. We acknowledge Pedro Cartagena for field assistance and Cecilia Hernández for drawing the figures.

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[3]Charles Darwin Research Station and Galápagos National Park Service, Santa Cruz, Galápagos, Ecuador.

FIGURE 1. Mature *Scalesia cordata* forest at site 3. Note the ground cover of ferns.

METHODS

Quadrats were established and marked with stakes in the corners, and all *Scalesia* trees were numbered. Twice a year (in April and October) height and girth (circumference at breast height) were measured. All measurements were undertaken by the same person (AT) the same way over the years. For the locations of the sites, see Figure 2.

DESCRIPTION OF THE STUDY SITES

Site 1. Known locally as "Alemania," 360 m. Evergreen forest with *Psidium guajava* L., *P. galapageium* Hook. f., *Zanthoxylum fagara* (L.) Sarg., *Tournefortia pubescens* Hook. f., *Acnistus ellipticus* Hook. f., and *Solanum erianthum* D. Don. *Scalesia cordata* trees are up to 10 m tall and one had a girth of over 0.80 m. Figures 3, 9b.

Site 2. Between La Sierra and Cerro Solitario, 220 m. Evergreen forest with *Psidium galapageium, P. guajava, Zanthoxylum fagara,* and *Tournefortia* spp. *Scalesia* trees are up to 8 m tall with a girth of less than 0.70 m. Figures 4, 10a.

Site 3. Known locally as "Callejón de La Sierra," 340 m. Evergreen forest with *Zanthoxylum fagara, Tournefortia pubescens,* and a few individuals of *Psidium guajava*. The site has a dominant stand of *Scalesia* trees shorter than 9 m and less than 0.50 m in girth. It has a 100% undergrowth of ferns (Fig. 1). Figures 5, 10b.

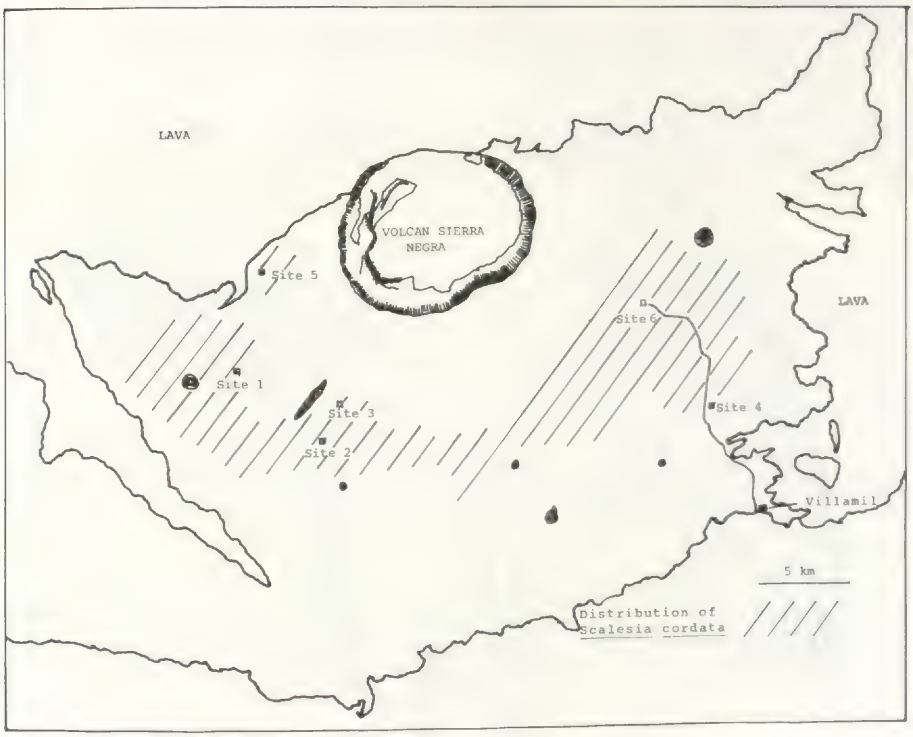


FIGURE 2. Location of the study sites on Volcán Sierra Negra, Isabela.

Site 4. At km 9 near the road from Villamil to Santo Tomás, 150 m. A dry deciduous forest with *Pisonia floribunda* Hook. f., *Croton scouleri* Hook. f., and *Opuntia insularis* Stewart; in this area *Scalesia cordata* and *S. affinis* meet. *Scalesia cordata* is less than 6 m tall with a girth under 0.25 m. Figures 6, 11b.

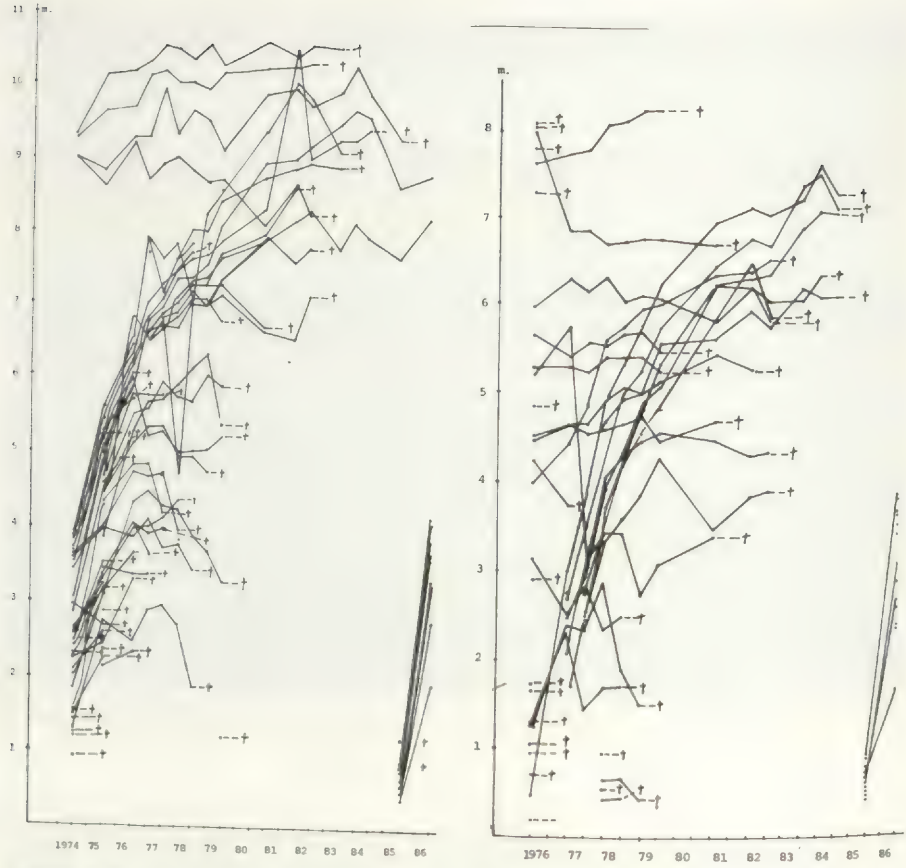
Site 5. Known locally as "zona de Velasco," 600 m. With *Zanthoxylum fagara* and *Tournefortia*. *Scalesia* trees do not grow taller than 5 m and the girth is up to 0.78 m. Figures 7, 11a.

Site 6. In the village of Santo Tomás, at the Corazón Verde experimental station, 350 m. Plantlets were transplanted from the farm zone and grew taller than 11 m with a girth of 0.55 m. This zone may have been one of the original main areas with *Scalesia cordata*. Figures 8, 9a.

RESULTS

Scalesia cordata is widespread on the southern slopes of Sierra Negra, ranging in altitude ca. 150–600 m.

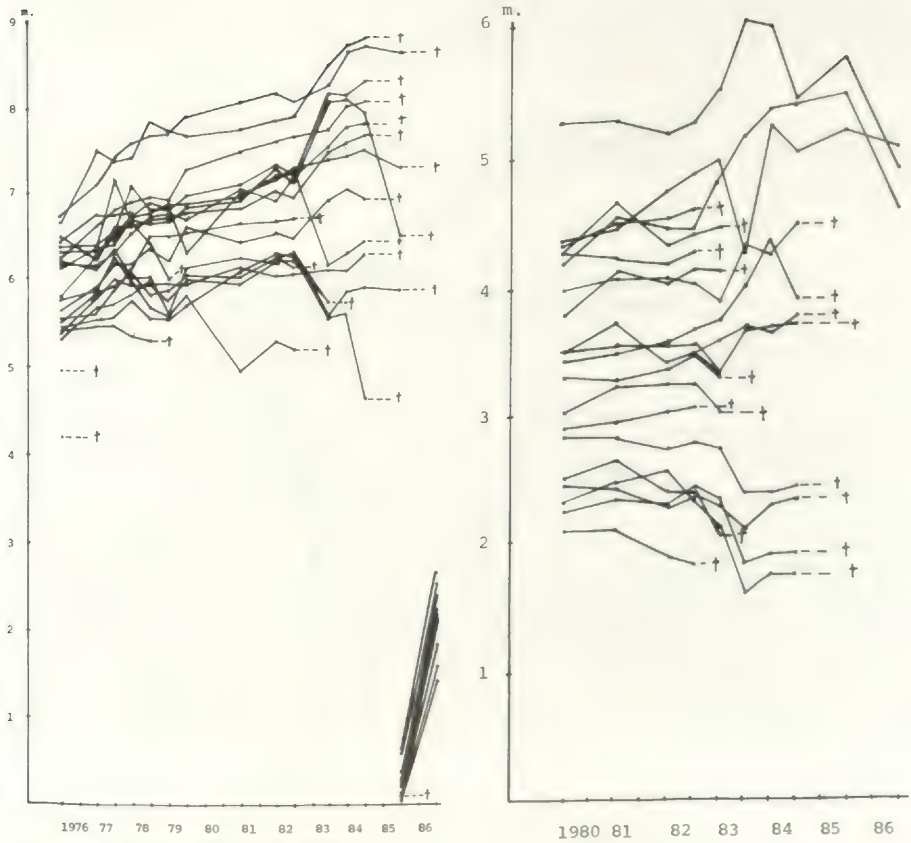
The growth rates of the trees in the different sites vary distinctively, as do the turnover rates. The sites 1, 2, and 3 had cohorts of plants emerging in 1985. In no other year did plants appear in cohorts except at site 1 in 1973 (extrapolated from data of 1974) and at site 2 in 1978 (observed) and in 1975 (extrapolated from data of 1976).



FIGURES 3–8. Growth curves of individual trees. Dashed lines indicate time of death (crosses). —3. Site 1. —4. Site 2.

Site 1. Three (and probably five) life classes can clearly be distinguished as cohorts of 1985, 1973, and four older trees, which could well be survivors of three earlier cohorts (two of 1960, one of 1949, and one of 1940). Three of these older trees died during the rains of El Niño, 1982–1983, whereas the fourth died in the drought of 1984–1985. Eight (20%) of the original 40 trees of the 1973 cohort survived until April 1982 (before El Niño); three were dead in October 1982, another two in April 1984, and one in October 1985. Only two trees survived El Niño 1982–1983 and the drought of 1984–1985. This plot had the tree with the greatest girth, 0.81 m; extrapolating on the base of the growth demonstrated in Figure 9b, this tree was 42 years old when it died in 1982. Using the relationship between height and girth (Fig. 12) the maximum age of this tree may have been 56 years.

In Figure 12 the averages for height and girth for the 1973 cohort are plotted, demonstrating the relationship of tree height to trunk circumference. The resulting curve resembles closely the relationship presented by Hamann (1979, p. 76) of a stand of *Scalesia pedunculata* recorded 1970–1977 on Santa Cruz. The habitat on site 1 of *S. cordata* is comparable to the site of Hamann's quadrat near the Caseta at Santa Cruz. The curve also fits closely the height/girth relation of one selected tree from site 6 (□ in Fig. 12) in a habitat very similar to site 1. In contrast, the curve of three

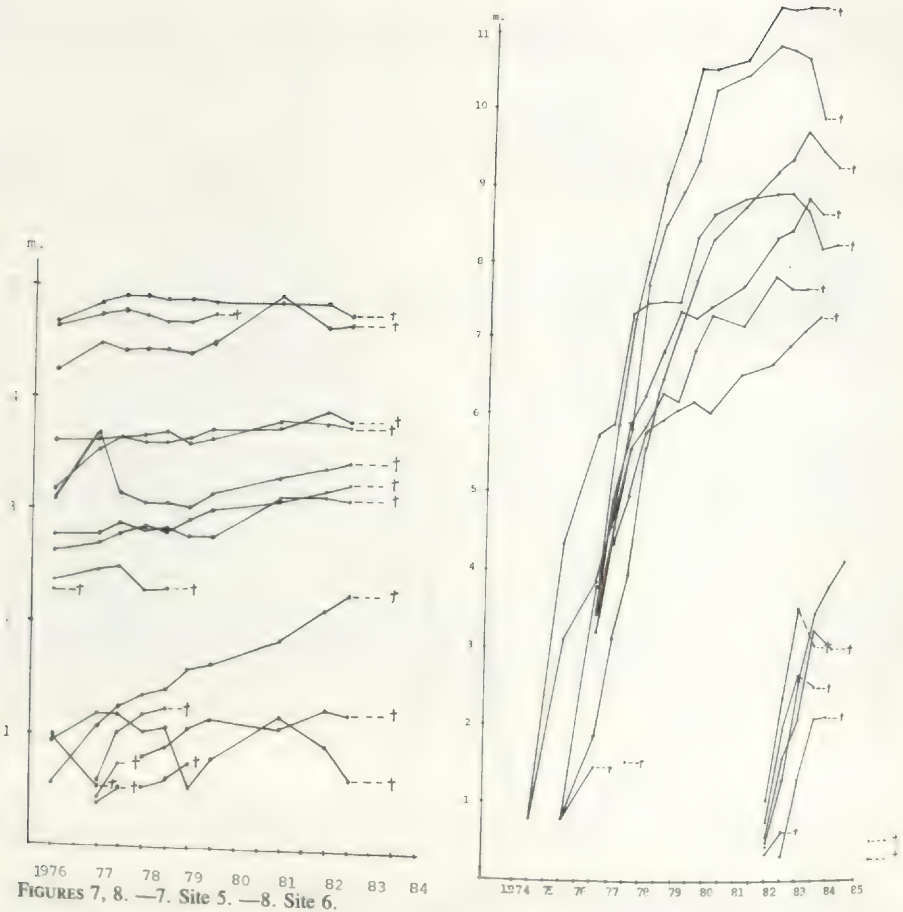


FIGURES 5, 6. —5. Site 3. —6. Site 4.

selected trees from site 5, a dry habitat, is very distinct (○ in Fig. 12). A tree on site 5 that is 5 m tall with a girth of 0.50 m is at least three times older than an 11-m-tall tree and with the same girth of 0.50 m at site 6.

Site 2. This plot was affected by the fires of April–June 1985. All trees died, probably by the combined effect of drought and fire. At least five (maybe seven) cohorts may be distinguished: those of 1985, 1978 (all died in 1978 or 1979), 1975, and two cohorts 4–6 m and 7–8 m tall, respectively. (Girth could be distinguished into four classes, 0.10–0.25; 0.35–0.45; 0.45–0.55; and 0.63–0.70 m.) Some trees from the 1975 cohort obtained a girth of 0.35 m within the first 10 years; from 0.35 to 0.45 m it took another 10 years, as did 0.45 to 0.55 m; for 0.55 to 0.63 m there are no data, whereas the growth of 0.63 to 0.70 m in 1.5 years is unusual. A tree with a girth of 0.70 m died in 1976, and could well have been 45–50 years old.

Site 3. This plot was affected by fires in 1985, and 13 remaining trees died. Three trees died during the rains of 1982–1983. When the plot was established in 1976 there was a mature forest of 22 trees 4–7 m tall and with girths of 0.15–0.41 m. During the ten years of observation (1976–1986) new plantlets emerged only in 1985; the ground cover of ferns apparently did not allow new plantlets to grow before this date. The growth in girth seems to be very small, and it is difficult to distinguish different life classes in the mature forest, although the trees are most likely of different ages. This



FIGURES 7, 8. —7. Site 5. —8. Site 6.

is not easy to explain, as the thick cover of ferns should not allow new cohorts to emerge in many different years. Growth of the girth suggests lapses of nine years for 0.20–0.25 m, 0.25–0.30 m, 0.30–0.40 m, and 0.40–0.50 m. When the quadrat was established, no trees under 4 m tall and with a girth under 0.15 m were observed, suggesting a minimum age of five years. The final age of the tree that died in 1985 with a girth of 0.50 m was probably 41 years old.

Site 4. The plot was established in 1980 with 20 trees of different ages, and life classes are difficult to establish. During the seven years of observation (1980–1986) no new plantlets emerged. Our data show dramatically the impact of El Niño 1982–1983 and the drought of 1984–1985: nine trees (45%) died in 1983 and eight (40%) in 1985; only three trees (15%) survived, two of which were the tallest and had the biggest girths (0.20–0.25 m) of the stand. In 1986 these two trees were most likely at least 24 years old, as girth growth from 0.05 to 0.10 m and 0.10 to 0.15 m were 5 years each, whereas growth from 0.15 to 0.20 m and 0.20 to 0.25 m were seven years each.

Site 5. This plot is distinct as it is away from the rest of the population of *Scalesia cordata* in a rather isolated area east of Sierra Negra. Thirteen plants were present when it was established in 1976; nine survived until 1982; all died with the rains in 1983. In 1977 and 1978, five new plantlets emerged, of which one survived until 1983. In this plot, there were many life classes, indicating that in many

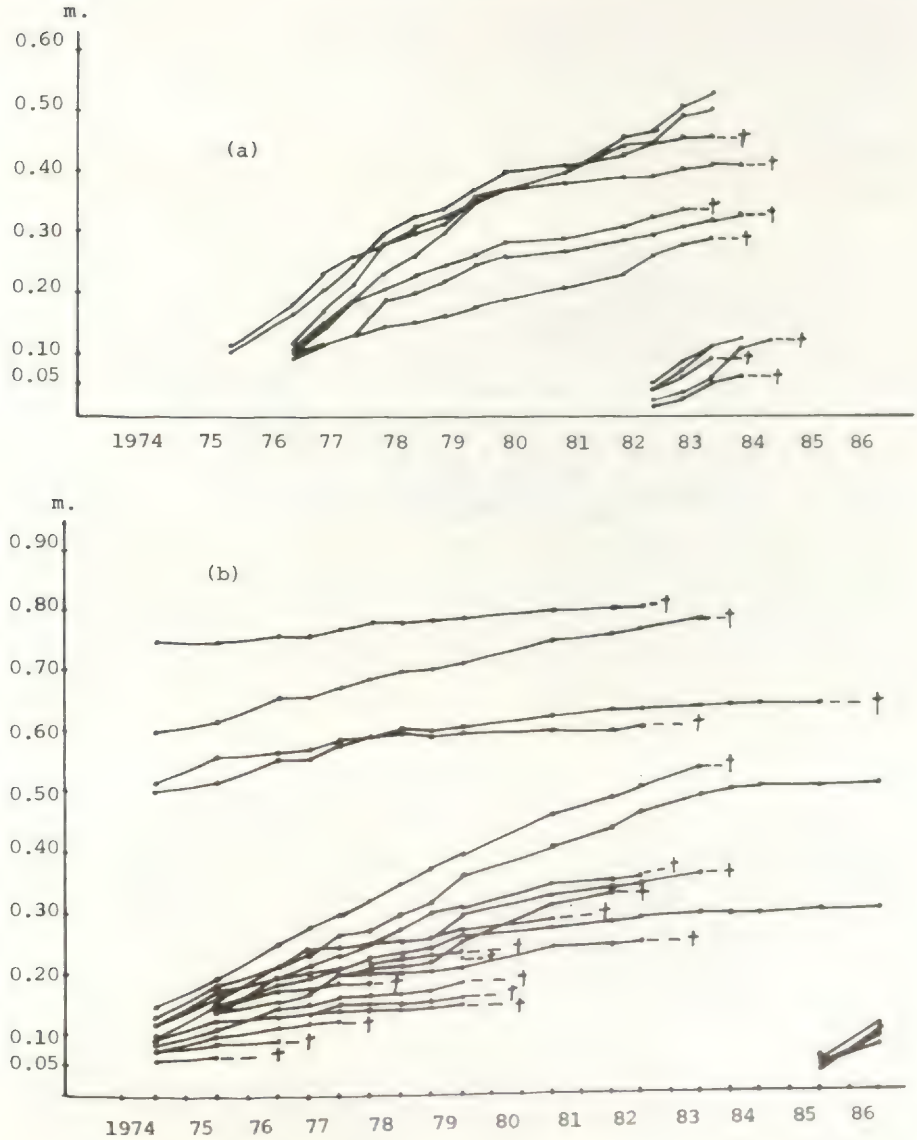


FIGURE 9. Growth of girth of individual trees at site 6 (a) and at site 1 (b).

years new plants became established. The growth curves for height (Figure 7) and girth (Figure 11a) indicate that in this area growth is very slow. Increase of the girth suggests lapses of 7 years for each of the categories 0.10 to 0.15 m; 0.15 to 0.20 m.; 0.20 to 0.25 m.; 0.25 to 0.30 m.; 0.30 to 0.40 m.; 0.40 to 0.50 m.; 0.50 to 0.60 m; and 0.60 to 0.70 m, with 0.05–0.10 m being reached in five years. The largest tree of the stand, with 0.78 m of girth, was estimated to be 65 years old when it died in 1980. In Figure 12 this large tree was plotted relating height and girth. Extrapolating the time span of girth growth of two other trees of different sizes of known age at the same site, the

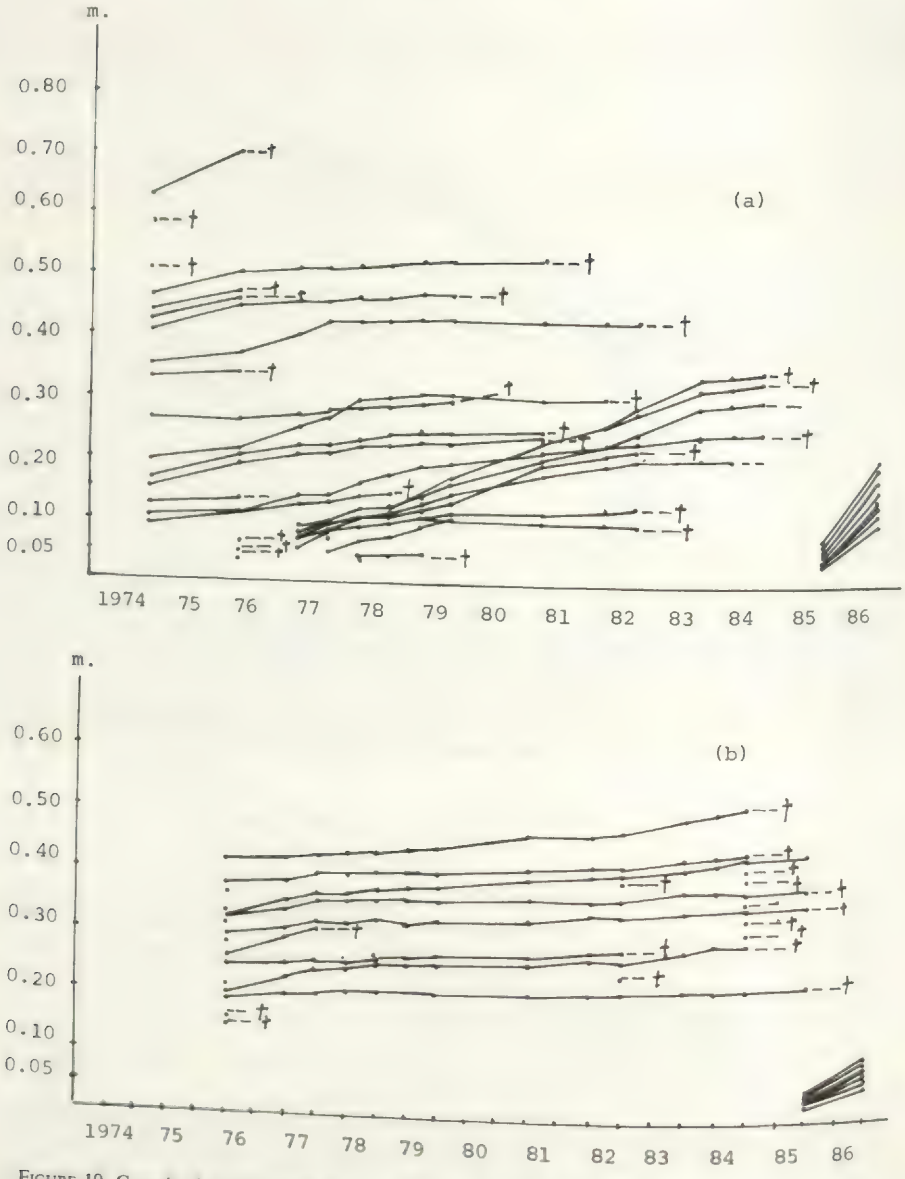


FIGURE 10. Growth of girth of individual trees at site 2 (a) and at site 3 (b).

minimum estimated age of the tree would have been 37 years. This difference can be explained by exceptional growth in 1977, when this large tree grew 5 cm in girth (see Fig. 11a).

Site 6. This is an experimental site, where 14 plantlets of *Scalesia cordata* were planted. Previous plots established in the cultivated zone were destroyed by cattle, the reason why data were obtained under experimental conditions. Growth curves of these trees are most similar to those of site 1. The tallest trees were found here, the maximum height was 11.45 m with a girth of 0.50 m; this tree was

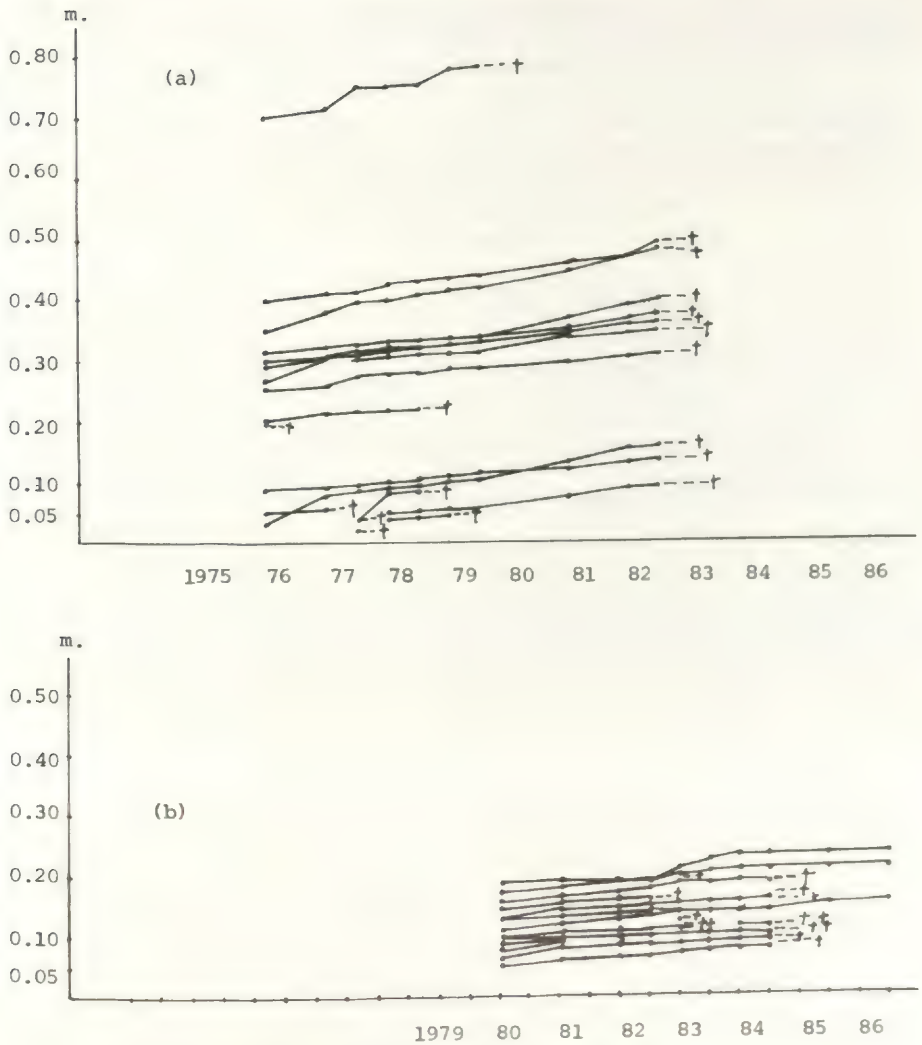


FIGURE 11. Growth of girth of individual trees at site 5 (a) and at site 4 (b).

10 years old when it died in 1984. All surviving trees died in 1983 (1) and 1984 (11) probably as a combined effect of the heavy rains of El Niño 1982–1983 and the drought of 1984, demonstrating that *Scalesia cordata* is not well adapted to such extreme conditions.

DISCUSSION AND CONCLUSIONS

Scalesia cordata is an opportunistic plant, quickly establishing in disturbed or otherwise open areas. Dispersion of *S. cordata* was not studied but is most likely similar to *Scalesia pedunculata* where it was shown that an isolated tree on San Salvador (Santiago) had hundreds of seedlings

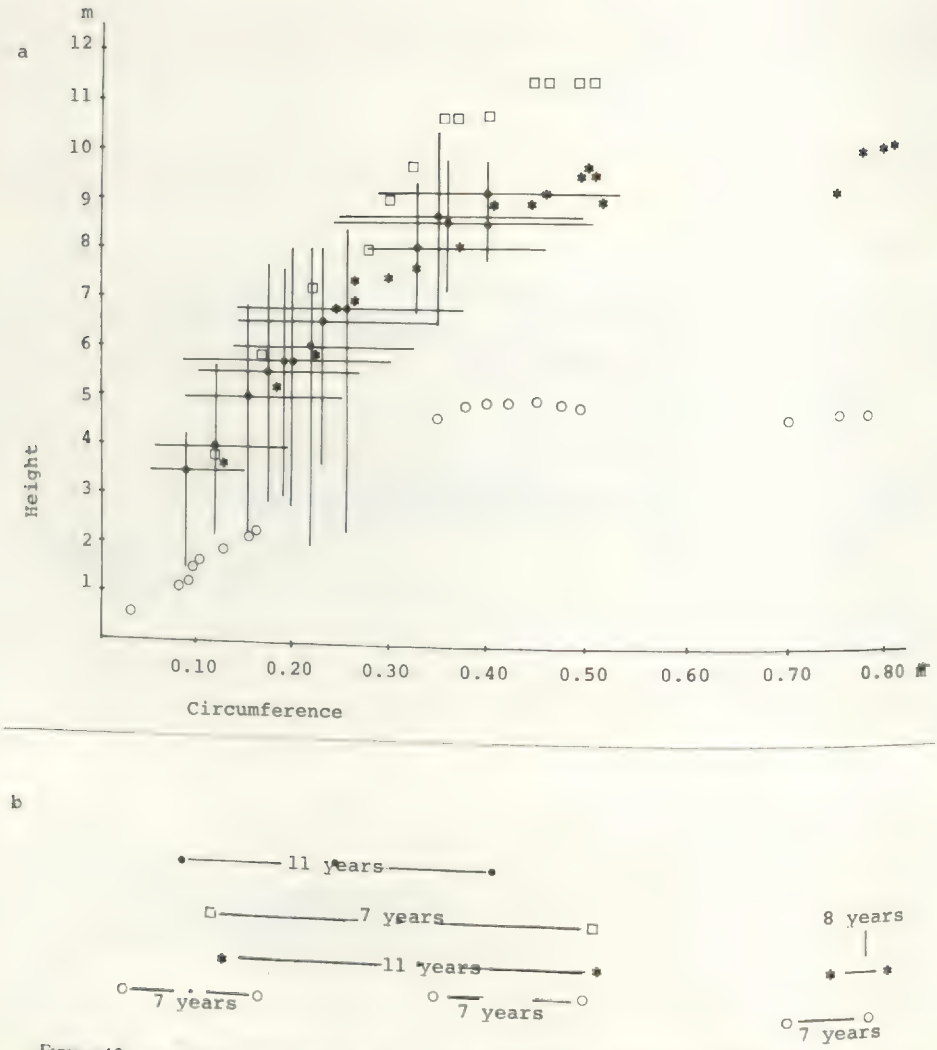


FIGURE 12. —a. Relationship of tree height to trunk circumference. Averages for cohort at same date; lines extend to maximum and minimum values. —b. Growth rate related to life span indicated in number of years. ● = cohort of 1973 at site 1 (N = 40, originally); ∗ = one tree of cohort of 1973 at site 1, and one old tree; □ = one tree at site 6; ○ = 3 trees at site 5.

growing around it in a radius of 15.50 m W, 15.40 m E, 20.50 m N, and 6.50 m S from the trunk (de Vries & Calvopiña, 1977). While *S. pedunculata* is confined to humid habitats, *S. cordata* ranges from humid to semiarid areas. This seems to result in different growth rates, life span, and survival strategies. They may produce flowers and seeds without producing seedlings over a long period of time. Other sites have an influx of new plants in several years, whereas at other places *Scalesia* emerges in cohorts each seventh year or more when some factors, probably drought, have opened grounds.

The *Scalesia cordata* trees may reach their maximum height of 11.5 m within 10 years. In dry

habitats trees were estimated to be 65 years old; in humid habitats ages were estimated to be slightly over 40 years. Noteworthy is the slow increase in girth of large trees (over 0.70 m) in humid habitats (site 1, * in Fig. 12) and the much faster growth in dry habitats (site 5; ○ in Fig. 12).

This difference is evident in Figure 12, where the growth rate is related to life span indicated in number of years for some individual trees. It was demonstrated that even in the humid habitat (site 1), most trees (85%) die in the first five years of life. At site 1 four old trees dominated until 1973 when a new cohort of 40 plantlets emerged. After 14 years only two trees still were alive, dominating in their turn until a cohort with more than 50 plantlets arose in 1985. These cycles could well follow the effects of the major climatic conditions after years of an El Niño.

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PERMANENT VEGETATION QUADRATS IN GALAPAGOS

Henning Adsersen[1]

ABSTRACT

To assess vegetation dynamics is highly relevant for conservation. In Galápagos, natural vegetation succession has been disrupted frequently by vulcanological and climatological events; and after humans' arrival with fire, alien plants and animals, and pesticides, additional disturbances occur regularly. Botanists have established several series of permanent quadrats to document vegetation development after disturbance in Galápagos; an account on their objective, location, methodology, and the publication of results is given.

Conservation of vegetation is not only a question of maintaining a status quo. It is much more a matter of keeping the dynamics of vegetation within natural succession patterns. When natural succession has been disrupted by external factors, vegetation conservation must also deal with the difficult tasks of assessment and control that lead back to natural vegetation.

Galápagos exhibits a long row of disruptions of natural successions. The disruptions may be natural as vulcanological events like lava flows (e.g., Marchena), pyroclastic deposits (Fernandina), upheaval (Urvina Bay), or geomorphological features like salt marsh or dune formation. Unusual climatic events like the 1983 El Niño cause great changes. Fires may be considered natural events (the destruction of some of Pinta's fern turf may be due to natural fire), but after humans' appearance most fires are human-caused: Santa Cruz in 1967 (de Vries, 1970), Sierra Negra in 1985. Humans brought and released, deliberately or by accident, alien animals, some of which caused general vegetation destruction (goats on all islands where they occur) or more or less partial changes, e.g., pigs eliminating terrestrial orchids (van der Werff, 1982) and lepidoptera that damage *Scalesia*.

The alien plants, intentionally or accidentally imported, may also cause vegetation scale changes (*Cinchona* on Santa Cruz, *Psidium guajava* on Sierra Negra, *Lantana camara* on Floreana, and *Eugenia* on San Cristóbal); disturb natural plant communities (alien species of *Passiflora*, *Kalanchoë*, and *Cleome*); or cause extinction of indigenous species (probably *Sicyos villosa* was wiped out by a disease brought in with cultivated Cucurbitaceae). On top of this, humans have manipulated considerable areas by means of agriculture, selective cutting, urbanization, gravel excavation, roads, tourism, and other activities.

Efforts to clear islands or parts of islands of some of the introduced aggressive organisms have opened the door for new successions, such as recovery of vegetation on islands where overgrazing pressure has been released, and we may even have to decide what to do on an island like Pinta, where vegetation now apparantly closes totally after the eradication of both the natural grazers, the tortoises, and the introduced ones, the goats.

Assessment of vegetation changes, successional or provoked by natural or cultural impact, has always been within the job description of the botanists attached to the CDRS, and almost all—de Vries, Hamann, Adsersen, Jeppesen, and Lawesson have initiated series of permanent vegetation quadrats to study the changes. However, due to the fact that the aims of the studies were different and that none of the botanists overlapped in time at the station, the approach to the study of dynamics of plant communities has not been consistent.

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Several authors have reported on achievements from their PQ studies (see reference list). The results give valuable information on many aspects of vegetation dynamics. On the population dynamics level, Hamann (1979) showed the surprising weedy character of *Scalesia pedunculata*, which dominates in evergreen forest tracts. De Vries & Tupiza (this volume) report on similar investigations on *S. cordata*, which to some extent vicariates for *S. pedunculata* on South Isabela.

On the plant community level, most publications deal with the impact of unusual or human pressure on the vegetation. De Vries & Calvopiña (1977) summarized the first years of a long-term study of the impact of goat and pig pressure on general diversity and on the recruitment of species dominant in the original vegetation. Hamann (1975, 1979a, 1984) reported in detail on the dynamics of revegetation after the eradication or decimation of goat populations on Pinta and Santa Fe, both with respect to diversity and dominant species. The enormous difference in rate of revegetation along the humidity gradient, and the role of the duration of the disturbance were emphasized.

After the eruption and caldera collapse of Fernandina in 1968, Hendrix (1981; Hendrix & Smith, 1986) studied revegetation from a denuded site, from damaged vegetation, and from an intermediate site. She reported on both diversity and on the processes governing the development (survival, immigration, and dispersal of the involved species).

The 1985 Sierra Negra fire was another catastrophic event with profound impact on vegetation. After the extinction of the fire, a system of PQs were set up and checked regularly, mainly by Nowak. A preliminary account is given in Nowak et al. (this volume).

Apart from the mentioned publications there exists a body of primary data and data reported only internally. These data as well as publications have obvious bearings on park management and research planning. The author is in the process of producing a catalog of permanent vegetation quadrats under previous or current study in Galápagos. In order to achieve a more comprehensive approach for future PQ studies approach, information will be given on:

1. Objective of study
2. Founder and establishment data
3. Location
4. Size and marks
5. Gross vegetation type
6. Methodology applied
7. Dates of checks, and checking scientists
8. Publications where the results have been presented

By means of the data and the results obtained so far we can add to an understanding of the dynamics of Galápagos vegetation. We must consider, though, that we have a rather poor representation of the various vegetation types. This holds true quantitatively (the area of the investigated PQs is very small in comparison with the area of the vegetation they represent) and qualitatively (many vegetation types and even some large islands have not been included). Furthermore, many PQs have been established in sites selected subjectively. What is needed to overcome this is transects through all vegetation types on a volcano (e.g., coast to top transects) along which PQs are placed according to preselected principles. Even if this takes place, there remains the problem of establishing reference PQs to study the development in areas free of the impact in question. In some of the studies, reference PQs have been established but sometimes with unexpected results. On Santiago, for instance, rats tend to accumulate in the fenced PQs because of the denser herb cover, and they may even reduce the survival of tree and shrub saplings to values lower than outside the fence (Calvopiña, pers. comm.). Similarly, we have observed that on Sierra Negra the unbalanced situation in the burnt area affects also the reference PQs on the unburnt side of the fire line (Nowak et al., this volume).

Vigorous climatic oscillations like the 1983 El Niño or the 1985 drought may cause much more drastic changes than the manageable factors under study (see Hamann, 1985, for a convincing example).

To locate PQs in the wilderness of Galápagos is a trivial but important problem. Personnel of the park service or CDRS should be involved in the fieldwork so that some resident in the islands knows the locations. For future PQ studies it is strongly recommended to apply squares of 10 × 10 m, to mark corners with stone piles or decomposition-resistant sticks, and to let sides run north–south and east–west. Indication of location should be in relation to obvious persistent marks in the field.

These critical remarks should not be read as advice not to set up PQ studies. On the contrary, there are no other ways to obtain exact and detailed information on the causes and processes in vegetation succession.

Apart from the permanent quadrats, hundreds or maybe thousands of relevés, stands, squares, or odd species compositions have been put down in notebooks. It would be very valuable if the catalog of permanent quadrats could be supplemented with information on when and where this sort of information has been gathered, and where these data are stored. It could be a first step to an exhaustive and contemporary treatment of Galápagos plant communities.

BRIEF LIST OF ISLANDS WHERE PQs HAVE BEEN ESTABLISHED

Española. A transect consisting of 11 PQs was established in 1977 by H. Adsersen and L. Calvopiña in the Gardner Bay area after the eradication of goats. Still being checked.

Fernandina. A transect of 11 PQs was established by Adsersen in 1974 on the vegetation strip on the western side. Still being checked.

Hendrix established a series of PQs on the rim in order to follow succession after the 1968 eruption. She reported on the study in 1981 (Hendrix, 1981) and shortly before her untimely death (Hendrix & Smith, 1986).

Floreana. Carvajal & Lawesson established in 1985 two PQs in *Scalesia* forest in order to study the cohort dynamics of *Scalesia pedunculata*. They have been checked several times during 1985–1987. The study also comprises similar PQs on San Cristóbal, Santa Cruz, and Santiago.

Gardner near Española. Five PQs on a transect on the northern slope, founded by Adsersen and Calvopiña, to serve as a reference for the Española transect mentioned above.

Pinta. De Vries established four PQs in 1970 and two in 1973 in order to follow the vegetation changes after the beginning of the goat eradication programs. The last check was by Hamann in 1988. Publications: Hamann (1975, 1979a, 1984); van der Werff (1978).

San Cristóbal. Carvajal & Lawesson established in 1985 two PQs in *Scalesia* forest in order to study the cohort dynamics of *Scalesia pedunculata*. They have been checked several times during 1985–1987. The study also comprises similar PQs on Floreana, Santa Cruz, and Santiago.

Santa Cruz. De Vries established PQs in the arid zone, the transition zone, the *Scalesia* zone, the *Miconia* zone, and the fern zone from 1966 to 1971. They were followed intensively until 1976, and some are still checked regularly by de Vries and Hamann. Publications: Hamann (1975, 1979b, 1984, 1985).

Adsersen established in 1974 a series of PQs along a 9-km-long transect from Puntudo northward to the Baltra road, which was opened the same year. Some of the PQs may be localized still, but the ones in the *Scalesia* zone were lost during the Niño year, 1983.

Carvajal and Hamann established in 1981 two PQs in remnants of *Scalesia* forest in the fern zone, and in 1985 Carvajal and Lawesson established five PQs in *Scalesia* forests in the whole range of its extension in order to study cohort dynamics of *Scalesia pendunculata*. They have been checked several times during 1985–1987. The study also comprises similar PQs on Floreana, San Cristóbal, and Santiago. Publications: Lawesson (1988).

In 1985, Ortiz & Lawesson established ten PQs in the highlands to study the advancing cover of *Cinchona succirubra*. Publications: Macdonald et al. (1988).

Santa Fe. Hamann established three PQs in 1972 and de Vries three in 1973 in order to follow regeneration of vegetation after the eradication of goats. The PQs are still being checked. Publications: Hamann (1975, 1979a, 1984, 1985).

Santiago. De Vries and Calvopiña established numerous PQs in order to study various aspects of goat and pig impact on the vegetation. Especially interesting are a number of fenced PQs with reference PQs outside the fences. They have been set up in the major vegetation zones and may be used also as pilot projects for gene pool exclosures. The PQs are currently checked. Publications: de Vries & Calvopiña (1977).

Carvajal and Lawesson established in 1985 two PQs in *Scalesia* forest in order to study the cohort dynamics of *Scalesia pedunculata*. They have been checked several times during 1985–1987. The study also comprises similar PQs on Floreana, San Cristóbal, and Santa Cruz.

Sierra Negra. De Vries and Tupiza established some PQs in 1974 in order to study population dynamics of *Scalesia cordata* and *Psidium guajava*. Some of the *Scalesia* quadrats were ravaged by the 1985 fire.

After this disastrous event a group with de Vries, Lawesson, Nowak, Tupiza, and Adsersen established approximately 50 PQs along the limits of the burnt area. Half of PQs are inside, and the other half are outside the burnt area. The PQs are currently under intensive studies. Publications: Nowak et al. (this volume, and various reports quoted there).

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THREATENED PLANT SPECIES AND PRIORITY PLANT CONSERVATION SITES IN THE GALAPAGOS ISLANDS[1]

Jonas E. Lawesson[2]

ABSTRACT

The status of the native Galápagos flora is evaluated in accordance with the IUCN Red Data Book categories. Two endemic species are believed to be Extinct, 20 taxa are Endangered, and 16 taxa seem to be Vulnerable. Also the numbers of rare native plants and numbers of plants in other IUCN categories are given. The localities with most threatened endemic and nonendemic taxa are given and used to identify the most important sites for conservation efforts. These key sites generally cover most of the important vegetation types in Galápagos. Combined autecological and synecological conservation measures are therefore recommended.

The status of the native flora and vegetation of Galápagos has attracted much concern during recent years due to the increasing impact from introduced plants, introduced animals, and humans, as documented by several authors (e.g., Adsersen, 1976, 1989; Calapucha & de Vries, 1980; Cruz et al., 1986; de Vries, 1977; de Vries & Calvopiña, 1977; de Vries & Tupiza, 1980; Eckhardt, 1972; Eliasson, 1968; Hamann, 1979, 1981, 1984; Kastdalen, 1982; Lawesson, 1986; Lawesson & Ortiz, this volume; Macdonald et al., 1988; Schofield, 1973; van der Werff, 1979). However, the basis for this concern has so far been fairly subjective, as no precise or objective way of evaluating the situation has been available. Efficient measures to improve the conditions for threatened taxa have therefore not been made, except in the most extreme and striking cases, such as on Santiago Island. This is simply due to the fact that it was unknown how endangered the taxon was, and where the last populations could be found. Some attempts have been made in recent years to approach this problem. D. Porter elaborated an unpublished Red Data Bulletin draft some years ago. The Conservation Monitoring Centre (CMC), of the International Union for Conservation of Nature and Natural Resources (IUCN), has for some time included in its database information on the endemics of Galápagos and their conservation status, organized according to the IUCN Red Data Book categories (Anonymous, 1980; Davis, this volume) as part of a global overview on plant conservation data. Although in need of updating, this database is useful for evaluating the Galápagos flora and its status. Adsersen (1989) provided another approach to evaluating the threatened plants. Not based on the IUCN categories, it evaluates population size and distribution of rare plants in Galápagos and the factors affecting wild populations. However, the term "rare" as Adsersen applied it is more broadly defined than what is usually seen, and is not directly comparable to the IUCN category. It is, however, a valuable contribution to the understanding of trends in the status of Galápagos plants.

In 1987 a conservation database which includes IUCN categories for all Galápagos vascular taxa (Fig. 1), was completed at the Charles Darwin Research Station (Lawesson, 1987a, b).

Based on the above references and field research carried out by the author and staff of the CDRS

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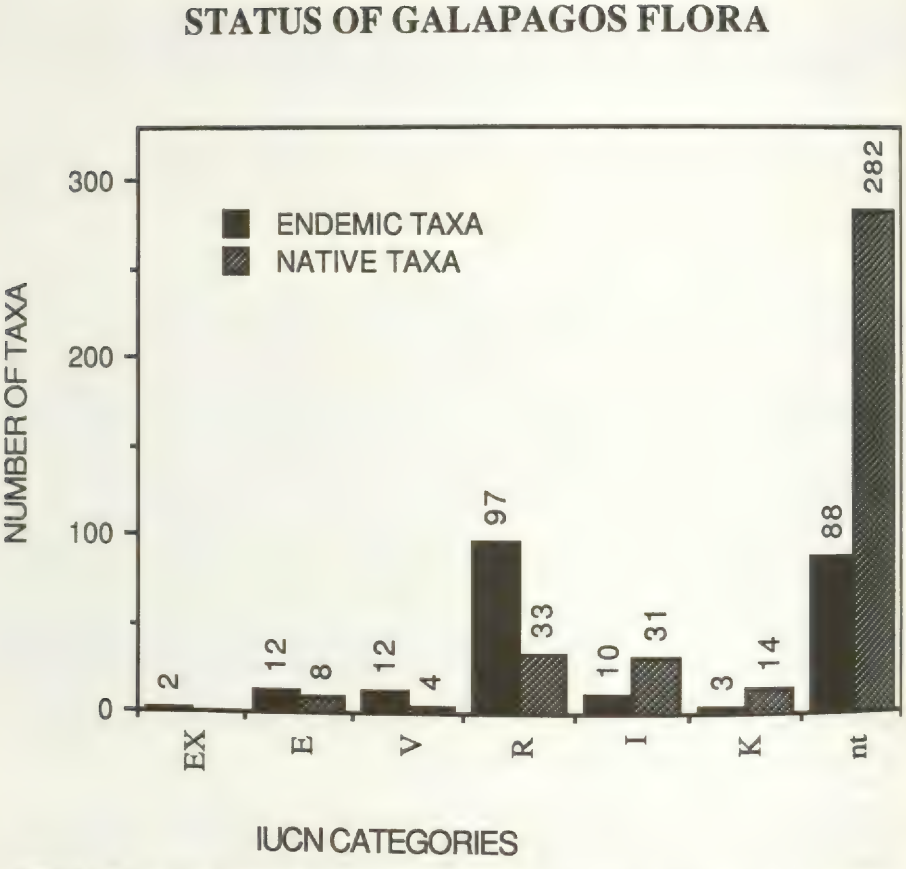

FIGURE 1. Status of the Galápagos flora, according to the IUCN categories. Ex = extinct, E = endangered, V = vulnerable, R = rare, I = indeterminate, K = insufficiently known, nt = not threatened.

1985–1987, this paper is an attempt to synthesize present knowledge. The approach is to describe the ecological status of the native flora of Galápagos with attention to endemic and nonendemic (from here on called native) taxa, reflecting the important roles of both groups in the plant communities of Galápagos. Special focus is on taxa most in danger of extinction; rare but not threatened taxa are mentioned briefly. The most endangered taxa are then pinpointed geographically, and the most significant sites for conservation of the threatened taxa have been identified (Fig. 2). A list of priority localities whose protection will ensure preservation of endangered taxa and vegetation types is presented. This includes plant communities otherwise not dealt with in the evaluation.

THE IUCN CATEGORIES

Seven categories are usually assigned when evaluating the status of a taxon (Anonymous, 1980). Ex (Extinct) is the category for taxa believed to be extinct after several searches in known and likely areas. E (Endangered) indicates danger of extinction and improbability of survival if the causal factors continue operating. V (Vulnerable) shows likelihood of slippage into the E category soon if the causal factors continue operating. R (Rare) is here used for taxa with small populations but not fitting any of the categories Ex, E, or V. I (Indeterminate) is for taxa known to be in one of the

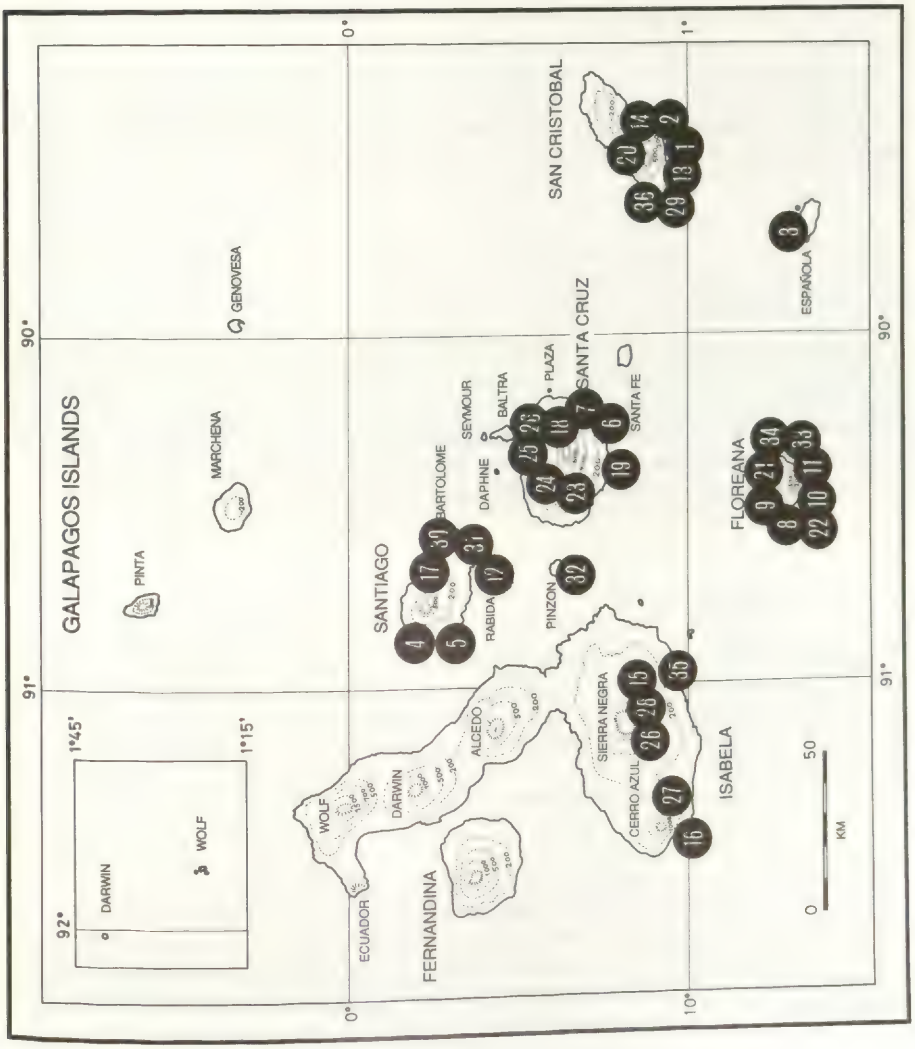

FIGURE 2. Map of key sites for threatened plants in Galápagos (categories E and V, as given in Table 1 and Table 2; numbers according to Table 1 and Table 2).

above-mentioned categories, but the information available is not sufficient to assign the correct category. Taxa classified as K (Insufficiently Known) are suspected but not definitely known to belong to any of the above categories. Taxa neither rare nor threatened are assigned to category nt. The above IUCN categories can be applied at any level, and an overall world category may be given to indicate the worldwide degree of threat. Categories Ex, E, V, R, and I are usually those included in Red Data Books and in lists of rare and threatened species. In this paper, however, as in the conservation database (Lawesson, 1987a), the categories have been applied to all the native and endemic taxa found in Galápagos, as an evaluation of the whole flora on an archipelago scale is of importance. Such an evaluation can reveal genetic erosion of a taxon.

Especially for the native taxa, the insular conservation status may be of great importance if the taxon is rare outside Galápagos, as is true for a number of threatened plants. In addition, the native taxa play a very important role in the species-poor vegetation of the Galápagos Islands. Conservation of Galápagos flora and vegetation is therefore equally important for native and endemic plants.

The Galapagos Flora

The concepts of the taxa vary among the different botanists involved in Galápagos botany, making an exact evaluation difficult. In general, however, Wiggins & Porter (1971) has been followed, except for new findings since 1971 and where recent generic revisions have included Galápagos plants. In a more complete account (Lawesson et al., 1987), it is stated that the native flora of Galápagos comprises about 596 taxa, of which 224 are endemic, and 372 are native. The distribution of these taxa in the different IUCN categories may be seen in Figure 1.

Extinct Galapagos Plants

Two endemic species from the Galápagos flora appear to be extinct. *Blutaparon rigidum* (Robinson & Greenman) Mears (1982), formerly known as *Philoxerus rigidus* J. Howell (Amaranthaceae), is known from Santiago, from which it has been collected twice, first by G. Baur in August 1891 and later by A. Stewart in 1905 or 1906. Baur's locality was the still-unlocated "Orchilla Bay" (Eliasson, 1985). Stewart's specimen came from the north coast of Santiago. Since then the species has never been found despite several searches (Eliasson, 1985; Lawesson et al., 1987). According to the categories, it must be considered Extinct. This may well be caused by the large population of goats on Santiago (80,000 animals, L. Calvopiña, pers. comm.) but also recent volcanic activity in the northern part of the island has been blamed for the extinction.

The endemic *Sicyos villosa* Hook. f. (Cucurbitaceae) from Floreana has not been found since the visit of Charles Darwin in 1835: "Charles Island, in great beds injurious to vegetation." Floreana was the first colonized island of the Galápagos Archipelago, and the introduction of alien plants and animals and direct destruction of the biota has left many changes. It has been suggested that disease introduced with the Common Cucumber *(Cucumis sativus)* may have exterminated *S. villosa* (Adsersen, pers. comm.). Whatever the reasons, *S. villosa* seems to be extinct, as several searches for this and other rare plants were made by the author in 1985–1987 together with Felipe Cruz, who has lived for many years on Floreana. The island continues to be heavily influenced by goats, cattle, and alien plant species (see Cruz et al., 1986; Lawesson & Ortiz, this volume); these conditions could be responsible for the extinction. Some authors claim other species to be extinct as well, but repeated searches for the mentioned taxa have not been reported. The taxa have therefore been allocated to the following categories.

TABLE 1. Galápagos taxa in danger of extinction (E Category).

ENDEMICS	
1 *Calandrinia galapagosa*	San Cristóbal
2 *Lecocarpus darwinii*	San Cristóbal
3 *L. lecocarpoides*	Española
Scalesia atractyloides	
4 var. *atractyloides*	Santiago
5 var. *darwinii*	Santiago
6 *S. helleri* subsp. *santacruziana*	Santa Cruz
7 *S. retroflexa*	Santa Cruz
8 *Alternanthera nesiotes*	Floreana
9 *Linum cratericola*	Floreana
10 *Lippia salicifolia*	Floreana
11 *Psychotria angustata*	Floreana
12 *Galvezia leucantha* subsp. *pubescens*	Rabida
NATIVES	
13 *Hemicarpha micrantha*	San Cristóbal
14 *Alternanthera rugulosa*	San Cristóbal
15 *Botrychium underwoodianum*	Isabela
16 *Cheilanthes myriophylla*	Isabela
17 *Doryopteris concolor*	Santiago
18 *Ranunculus flagelliformis*	Santa Cruz
19 *Fimbristylis littoralis*	Santa Cruz
20 *Lycopodium phylicifolium*	San Cristóbal

TABLE 2. Vulnerable Galápagos taxa (V category). Numbering continued from Table 1.

ENDEMICS	
21 *Lecocarpus pinnatifidus*	Floreana
22 *Opuntia megasperma* var. *megasperma*	Floreana
23 *Heliotropium andersonii*	Santa Cruz
24 *Acalypha wigginsii*	Santa Cruz
25 *Miconia robinsoniana*	Santa Cruz, San Cristóbal
26 *Pernettya howelli*	Santa Cruz, Isabela
27 *Cranichis lichenophila*	Isabela
28 *Darwiniothamnus alternifolius*	Isabela
29 *Scalesia gordilloi*	San Cristóbal
30 *S. stewartii*	Santiago
31 *Mollugo crockeri*	Santiago
32 *Verbena grisea*	Pinzon
NATIVES	
33 *Buddleja americana*	Floreana
34 *Galium reynoldsii*	Floreana
35 *Ipomoea stolonifera*	Isabela
36 *Juncus pallescens*	San Cristóbal

ENDANGERED AND VULNERABLE GALAPAGOS PLANTS

Twenty taxa in Galápagos are so far known to be in ultimate danger of extinction, and in need of urgent, protective measures. Twelve endemic and eight native taxa belong to the E category (Table 1), whereas 12 endemic and four native taxa are believed vulnerable (Table 2).

Asteraceae, with the genera *Scalesia* and *Lecocarpus*, seem to be the family with most taxa in a critical state, with, in total, six and three taxa in the E and V categories, respectively.

SCALESIA

Being endemic for Galápagos, *Scalesia* comprises 15 species and 21 taxa (Eliasson, 1974; Hamann & Wium-Andersen, 1986) and an additional taxon probably needs to be described (Lawesson & Adsersen, 1987). The genus includes trees (*S. pedunculata* Hook. f., *S. microcephala* Robinson, and *S. cordata* Stewart) in the highlands of the larger islands. Most scalesias, however, are found in the relatively dry lowlands, especially along the coasts where several members of *Scalesia* have evolved; these taxa are restricted to small areas and have probably always occurred in small populations. Now, such taxa nearly all appear to suffer from grazing of introduced animals, although a few still remain out of threat, e.g., *Scalesia affinis* Hook. f.

Four coastal taxa of *Scalesia* belong to the E category: two varieties of *S. atractyloides* Arn. are found in westernmost Santiago; *S. atractyloides* var. *atractyloides* and var. *darwinii* (Hook. f.) Eliasson of this species have been known for some time from Buccanero Cove to Cerro Trebol close to Bahia Sullivan, and Stewart (1911) reported *S. atractyloides* to occur up to 300 m. Without doubt, the feral goats have now depleted these two varieties of *Scalesia atractyloides* severely. Recent searches by the author revealed that *S. atractyloides* no longer survives around Buccanero Cove, while in James Bay declining (L. Calvopiña, pers. comm.) populations of about 10 individuals each exist on two small hills. An optimistic estimate would therefore be 50 plants of each taxon. Populations of such size probably cannot sustain themselves for long, particularly as the goat predation is continuing. Indeed, this situation was already described 20 years ago (Eliasson, 1968). Calvopiña, Toro, and Adsersen in 1985 transported seeds from the two populations to a fenced area in Buccanero Cove, but apparently no seedlings emerged (Adsersen, pers. comm.).

Scalesia retroflexa Hemsley and *S. helleri* Robinson subsp. *santacruziana* Harling occur at the south coast of Santa Cruz and are equally endangered, probably due to goat predation. *Scalesia retroflexa* is known only from a few localities around Punta Nuñez, at the southeastern point of the island. In 1986 it appeared to be restricted to some few coastal cliffs and one small inland population. *Scalesia helleri* subsp. *santacruziana* occurs around Bahia Tortuga, where it is restricted to steep-cliff refugia from goats (Eliasson, 1974). By 1986 this situation had not changed. Both taxa have dwindled to fewer than 50 individuals, but exact counts, which should be made without hesitation, may show even smaller population sizes.

Additionally, *Scalesia gordilloi* (Fig. 3) (Hamann & Wium-Andersen, 1986), from the south coast of San Cristóbal, and *S. stewartii* H. Riley, from the east coast of Santiago, are placed in the V category.

LECOCARPUS

The genus *Lecocarpus* is endemic to Galápagos and comprises three species (Adsersen, 1980), all in the threatened categories. The situation appears to be most critical on San Cristóbal, where *L. darwinii* Adsersen occurs. It has been found in four localities (Bahia Rosa Blanca, Cerro Verde, Cerro Pelado, and Cerro Brujo), but a growing population of feral goats apparently browse on this species, which now is believed to be in danger of extinction.

The same is the case of *L. lecocarpoides* Cronq. & Stuessy only known from Española and the islets in Gardner Bay. The goats were eliminated from Española in 1978, but, due to their long presence on the island—at least since 1905 (Hoeck, 1984)—the impact on the flora and vegetation presumably has been great. Since the eradication of the goats, one population of four plants of *L. lecocarpoides* has been known from the landing beach at the northern coast. A modest regeneration by means of seedlings has been observed by Adsersen in 1974, 1977, and 1985, and by the author in 1986. However, the new seedlings seem to have difficulties reaching the shrubby stage. On Gardner and the other islets in Gardner Bay, the situation is stable, as no goats were ever present

FIGURE 3. *Scalesia gordilloi* from San Cristóbal.

there. However, Gardner is small, and the *Lecocarpus* plants probably only represent a fraction of the original population found on Española. Considering that small populations on small islands must be especially vulnerable to environmental changes, it is believed that *L. lecocarpoides* belongs to the endangered plants of Galápagos, although modest optimism is justified.

Yet another threatened species of the genus is *Lecocarpus pinnatifidus* Decme (Fig. 4), which inhabits the humid highlands of Floreana. Its range has been decreasing during recent years due to the invasion of introduced plants, especially *Lantana camara* L. (Cruz et al., 1986; Lawesson & Ortiz, this volume). It is still known from some localities, especially Point Comorant, but is suffering from the increasing goat population on Floreana, about 10,000 animals in 1987. *Lecocarpus pinnatifidus* is therefore assigned to the Vulnerable category (V).

GALVEZIA

The genus *Galvezia* (Scrophulariaceae) is represented by two subspecies in Galápagos, of which *G. leucantha* subsp. *pubescens* Wiggins is in danger of extinction. This subspecies is only found on the small island of Rabida, to which goats were introduced in 1971 but apparently eradicated later the same year. Despite removal of the goats, the subspecies appears in very low numbers, between 10 and 50, and is believed to be unable to sustain itself at such a small population size.

OTHER ENDANGERED AND VULNERABLE PLANTS

FLOREANA

The invasion of the highlands on Floreana by alien species is threatening other endemic species, besides *Lecocarpus*. This is the case for *Linum cratericola* Eliasson, *Psychotria angustata* Anders-

FIGURE 4. *Lecocarpus pinnatifidus*, only known from Florena and its islets, an Endangered species.

son, and *Lippia salicifolia* Andersson, all restricted to the area around Cerro Pajas in the central highlands. The *Linum* species was sought in vain in April 1987 at the type locality by Uno Eliasson, and is feared to be Extinct. *Psychotria angustata* (Fig. 5) was reported by Eliasson (1982), and was found by the present author and Felipe Cruz in 1986. Some few plants are known from the Pajas Crater as well as from a nearby sinkhole. *Lippia salicifolia* has been known by the colonists on Floreana for long as the "unknown tree." It was abundant 50 years ago, when some of the settlers used it for house constructions (pers. comm. from family Cruz). A preliminary estimation in 1987 indicated that a maximum of 50 adult trees of 5–10 m tall exists in the central agricultural area and the National Park area close to Cerro Pajas. An abundant growth of seedlings was noticed in March 1987, but it is feared that most of this regeneration will be destroyed by free-ranging cattle and goats.

Additional species are found in the highland, still in reasonable numbers, but in a state causing concern. This is the situation for *Buddleja americana* L. (Lawesson & Norman, 1987; Norman & Lawesson, 1988), and *Galium reynoldsii* Dempster (Lawesson, 1988), two recently discovered native plants for Galápagos. They are considered to belong to the V category.

Although most taxa in the Endangered or Vulnerable categories are found in the highlands, there are also problems in the lowlands, where severe destruction by goats and other introduced herbivores affects the structure and the components of the vegetation. Prominent features like cacti (*Opuntia megasperma* Howell var. *megasperma*, V category) are becoming less common, and large areas remain without much vegetation in the dry season. One species so far is in danger of extinction here, *Alternanthera nesiotes* J. M. Johnston, and others may become so in short time.

SAN CRISTOBAL

San Cristóbal houses two endemic plants in the coastal areas facing extinction. *Lecocarpus darwinii* (mentioned above) occurs with *Calandrinia galapogosa* St. John in the dry coastal low-

FIGURE 5. *Psychotria angustata* from Floreana, probably one of the endemic species most in danger of extinction.

lands, which are characterized by deciduous steppe forest vegetation types. *Calandrinia galapogosa* has its main populations at Cerro Verde and Sappho Cove, on the northern half of the island. Eliasson (1968) reported on this plant from Sappho Cove, where 20 bushes were found, "all plants sterile and severely browsed." "I consider this species to be threatened by extinction if no measures are taken to prevent continuous browsing." Adsersen (pers. comm.) observed it in 1977 at Cerro Pitt and Bahia Rosa Blanca. The succulent plant is still severely browsed by the expanding goat population, and it now survives only on vertical, inaccessible cliffs (pers. obs.). The CDRS representative on San Cristóbal, J. Gordillo, transplanted it to his garden, where it flowered. Ex situ conservation is therefore possible.

The highland vegetation types are changing and their original floristic elements are being depleted and becoming threatened due to the invasion of alien plants and agricultural use of former forest areas as described by van der Werff (1979), Lawesson & Estupiñan (1987), and Gordillo (this volume). *Hemicarpha micrantha* Britton has not been found recently. *Alternanthera rugulosa* Howell was recently found by S. Itow and the author in the gorge of La Honda, and sporadically on four other localities. It probably formed a part of the evergreen forests on this island, now gone and taken over by the introduced *Psidium guajava* L. Also worth mentioning are the native *Juncus pallescens* Lamarck and *Lycopodium phylicaefolium* Desv. recently found around the El Junco Lake (H. Adsersen, pers. comm.). They are vulnerable due to the impact from free-ranging cattle.

SANTA CRUZ

The *Scalesia* taxa mentioned earlier and a number of other plants are threatened on Santa Cruz. *Fimbristylis littoralis* Gaud., a native collected close to Academy Bay, has not been found for many years and may already be extinct, or is extremely rare. In the highlands, *Ranunculus flagelliformis*

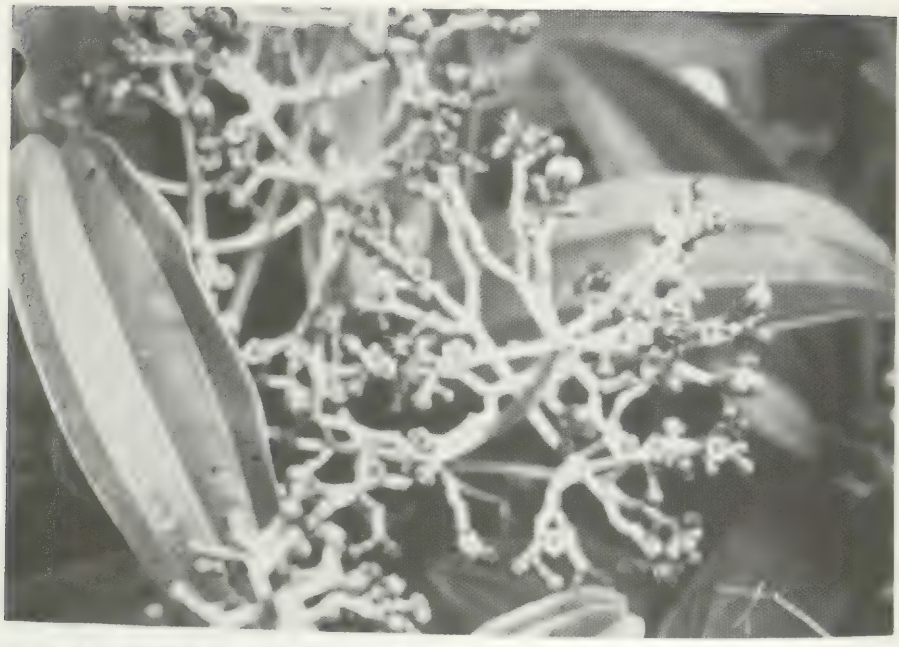

FIGURE 6. *Miconia robinsoniana* is only known from the highlands of Santa Cruz and San Cristóbal and is threatened by agricultural settlements and invasive alien plants.

Smith is Endangered. This only representative of the Ranunculaceae in Galápagos exists in a few temporary pools close to Cerro Puntudo and on Cerro Crocker, and the population could easily be eliminated by invasion of introduced plants or by heavy grazing. Other species from this area are the endemics *Miconia robinsoniana* Cogn. (Fig. 6.), *Pernettya howellii* Sleumer, and *Acalypha wigginsii* Webster, all found in the highest part of the island and considered Vulnerable. The current precarious status of many native and endemic taxa in the highlands of the island may be caused by frequent fires in the area, reported from 1934, 1946, 1947, 1959, 1961, 1965, and 1968 (Y. Carvajal & T. de Roy, pers. comm.; Eckhardt, 1972; Kastdalen, 1982). *Heliotropium andersonii* Robinson was earlier found in the dry and transition zones (sensu Wiggins & Porter, 1971). It was found at Cerro Dragon in 1987 (Adsersen, pers. comm.) but has apparently become very rare.

ISABELA

This island remains largely in a pristine state, except for the southern part, which comprises the volcanoes Sierra Negra and Cerro Azul, where human settlements, free-ranging cattle, and fires have changed the vegetation considerably, probably from an original shrubby vegetation with trees to the present secondary herb meadow vegetation (see, e.g., Nowak et al., this volume). The disturbance in the area is probably responsible for the Vulnerable status of the recently described *Darwiniothamnus alternifolius* (Lawesson & Adsersen, 1987), which occurs on both volcanoes. Two native ferns are Endangered, namely *Botrychium underwoodianum* Maxon and *Cheilanthes myriophylla* Desv., found on Sierra Negra and Cerro Azul, respectively. The orchid *Cranichis lichenophila* D. Weber from Cerro Azul is considered Vulnerable, as is the recently found beach plant *Ipomoea stolonifera* (Cyrill.) Gmel, which grows within the limits of the village of Villamil.

FIGURE 7. The highlands of Santiago, formerly covered by evergreen forests; now only scattered trees are found.

where traffic and use of sand for construction may deplete the population of this plant in the coming years.

SANTIAGO

Two vulnerable plants from Santiago should be mentioned: the endemic *Mollugo crockeri* Howell, from the coast, and the native *Doryopteris concolor* Kuhn, in the highlands. Neither of these two species have been found recently (Fig. 7).

PINZON

On this island, the endemic *Verbena grisea* Robinson & Greenman is found at one locality. The reason why the population is so small is not known, but the large population of black rats could be responsible, since it has been shown that black rats may eat many plants (Hoeck, 1984). *Verbena grisea* is placed in the Vulnerable category.

RARE PLANTS IN GALAPAGOS

Many endemic taxa in Galápagos are rare. This is not surprising, as most endemic species per definition are restricted geographically. It is also typical for some endemic plants to have very small populations. This obviously makes them more vulnerable to natural and man-made environmental changes. However, it is important to stress that rare is not equal to threatened. The native nonen-

TABLE 3. Key sites for Galápagos based on E and V taxa occurrence.

Locality	Vegetation type	Threatened taxa
ISABELA		
Beach, Villamil	sand dune	*Ipomoea stolonifera*
Cerro Azul	deciduous forest	*Cheilanthes myriophylla*
Cerro Azul	evergreen scrub	*Cranichis lichenophila*
Sierra Negra	deciduous forest	*Botrychium underwoodianum*
Sierra Negra	fern/grass meadow	*Darwiniothamnus alternifolius*
SANTA CRUZ		
SE coast	deciduous forest & coastal cliffs	*Scalesia helleri* *S. retroflexa* *Fimbristylis littoralis*
S slope	dry zone vegetation	*Heliotropium andersonii*
Puntudo	fern/grass	*Acalypha wigginsii*
Cerro Crocker	temporary pools	*Ranunculus flagelliformis*
FLOREANA		
Coasts	dry deciduous vegetation	*Opuntia megasperma* *Alternanthera nesiotes*
Highlands	evergreen scrub and forest	*Lecocarpus pinnatifidus*
	evergreen forest	*Linum cratericola* *Buddleja americana* *Galium reynoldsii* *Lippia salicifolia* *Psychotria angustata*
SANTIAGO		
Coasts	coastal desert	*Scalesia atractyloides* *S. stewartii* *Mollugo crockeri*
Highlands	evergreen forest	*Doryopteris concolor*
SAN CRISTÓBAL		
Coasts	desert scrub	*Calandrinia galapagosa* *Lecocarpus darwinii* *Hemicarpha micrantha*
La Honda River	evergreen forest	*Scalesia gordilloi*
Cerro San Joaquin	evergreen scrub	*Alternanthera rugulosa*
El Junco area	grass/fern meadow	*Miconia robinsoniana* *Juncus pallescens* *Lycopodium phylicifolium*
ESPAÑOLA		
Coast	coastal scrub	*Lecocarpus lecocarpoides*
RABIDA		
Coastal cliffs	desert scrub	*Galvezia leucantha*
PINZON		
Central part	deciduous forest	*Verbena grisea*

demic plants, on the other hand, are often found in larger areas and will therefore usually be less sensitive to changes. Thirty-three native taxa are considered Rare, but most rare Galápagos plants are among the 97 endemic taxa.

A group of taxa belong to the I and K categories, as they are not known to be threatened at present, although the knowledge is insufficient. Very few endemics are found in these two categories. This is natural, as the distribution and population size of the endemic taxa usually are better known than for the native taxa.

TABLE 4. Additional key sites for protection of special vegetation types.

Island	Vegetation type/community
SAN CRISTÓBAL	
La Honda River	Unique fern and moss vegetation
El Junco Lake	*Utricularia* lake
Cerro San Joaquin	Sphagnum bogs
SANTA CRUZ	
Cerro Crocker	Sphagnum bogs and fens *Cyathea* thickets
Agricultural zone	Brown zone

THE NONTHREATENED FLORA

The known nonthreatened plants (nt category) in Galápagos comprise 370 taxa. Many endemic plants are common and will probably never become threatened, such as *Pisonia floribunda* Hook. f., *Scalesia affinis*, *Justicia galapagana* Lindau, *Castela galapageia* Hook. f., *Psidium galapageium* Hook. f., and *Macraea laricifolia* Hook. f.

THE KEY SITES AND THE RELATED VEGETATION TYPES

The essential key sites for the Endangered and Vulnerable Galápagos plants are indicated in Figure 2. Many threatened taxa are found on Floreana, Santa Cruz, Santiago, and San Cristóbal, and fewer on Isabela, Rabida, and Pinzon. In Table 3 is indicated the vegetation type for the area in which each given taxon is found. The important vegetation types are covered for each island. They include deciduous forest, coastal cliffs, desert scrub, evergreen scrub, evergreen forest, fern-sedge meadow, and temporary pools. Only some particular plant communities dominated by bryophytes and lichens, such as the bogs in the highlands, do not enter into this account; nevertheless, they should be included in conservation and management considerations because these communities are rare and unique in Galápagos (Itow & Weber, 1974). They seem to be threatened by general habitat destruction and probably drier microclimate due to deforestation as seen on San Cristóbal (Lawesson & Estupiñan, 1987) and Santiago. The same is true for the *Cyathea* thickets, which are in decline. Other special communities are the few permanent limnic environments, such as El Junco Lake and The Honda River on San Cristóbal. With their special plants and animals, they should be included in a list of the potential key sites for protection. Such additional vegetation types have been listed in Table 4.

CONCLUSION

Many Galápagos endemic and nonendemic plant species are threatened by introduced animals and plants and by human impact; a number of taxa will definitely become extinct in a short time if adequate conservation measures are not implemented soon. Almost all Endangered species are concentrated on the populated islands of Floreana, San Cristóbal, Santa Cruz, Southern Isabela, and on Santiago. With the extinction of typical Galápagos plants, typical plant communities and vegetation zones will also become rare or extinct. The brown zone, previously abundant on Santa Cruz, is now restricted to a small area on the north slope of the island, whereas the *Miconia* and *Scalesia* zones on San Cristóbal have been destroyed almost completely. These types of vegetation are the more obvious examples, but many more are facing similar status. In general, the way of relating autecological with synecological conservation, as suggested in this paper, seems to be a feasible

way of protecting sites of highest scientific and conservation priority. The key sites for conservation action, as suggested in this paper, should be protected in an appropriate way (fencing, control of introduced plants, limits on human intervention) as soon as possible in order to conserve a representative part of the Galápagos flora and vegetation types, while this is still possible.

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THE IMPACT OF INTRODUCED HERBIVORES ON THE GALAPAGOS RAIL (*LATERALLUS SPILONOTUS*)[1]

Daniel K. Rosenberg[2]

ABSTRACT

The Galápagos rail (*Latterallus spilonotus*) is known from seven islands in the archipelago. By affecting the ground vegetation, introduced herbivores, which live on six of the islands, are likely to affect rail populations. The results of a census made during 1986–1987 on six of the seven islands showed the Galápagos rail common only on the upper regions of Santa Cruz and southern Isabela islands. Pinta Island was not checked but the rails are believed to be common there. Rails were found on Fernandina Island, but the availability of suitable habitat likely limits the population to small numbers. Rails were very rare on San Cristóbal and were not found on Floreana. Rails were restricted to a few small sites on Santiago and were found less often than expected by chance in areas with herbaceous vegetation cover shorter than 30 cm tall, which appeared to be extensively grazed by feral goats (Bovidae). There is likely to be selection against use of low cover through predation by a large number of potential predators. Conservation of the native highland flora will likely benefit the Galápagos rail populations.

Students of Galápagos botany have expressed a great concern about the damage to the indigenous flora by introduced herbivores (Eliasson, 1968; Weber, 1971; Hamann, 1975, 1979a, b, 1981, 1984; Adsersen, 1976; de Vries & Calvopiña, 1977). Goats, cattle (Bovidae), horses (Equidae), donkeys (Equidae), and pigs (Suidae) are known to destroy island vegetation (Coblentz, 1978; Ralph & van Riper, 1985). By selective grazing, introduced herbivores may affect the flora by changing the frequency of plant species and by increasing the opportunities for invasion by introduced species (Hamann, 1979a). Birds are differentially affected by these changes: some will increase, others will decline (see Bock & Webb, 1984).

Ground-dwelling birds are more likely to be adversely affected than other groups, as damage to undergrowth vegetation is likely to be more severe, and trampling of nests may occur (see Coulter et al., 1985, for the dark-rumped petrel, *Pterodroma phaeopygia*). Several species of rails (Rallidae) appear to have been negatively affected by damage to ground cover (e.g., *Tricholimnas sylvestris;* King, 1981). Many island forms of rails occur, and this combined with their ground-nesting habits makes them a particularly vulnerable group. King (1981) listed 18 species of rails that are believed to have become extinct since 1600. All were endemic island forms. Currently, 16 extant species are considered endangered or threatened (King, 1981). With few exceptions, they occur on islands. Habitat destruction from introduced herbivores and human development, and predation by exotic mammals (e.g., rats (Muridae), cats (Felidae), and pigs), are believed to be largely responsible for the high number of threatened, endangered, or extinct rails (Baldwin, 1945; King, 1981, 1985; Atkinson, 1985).

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The endemic Galápagos rail (*Laterallus spilonotus*) is found on seven islands within the Galápagos Archipelago (Franklin et al., 1979). They occur only on islands with humid-zone vegetation; of these, Santa Cruz, Isabela, San Cristóbal, and Floreana have a permanent human population, and Santiago was temporarily inhabited and currently has a large feral goat and pig population (L. Calvopiña, pers. comm.). Of the remaining islands where the rail occurs, Fernandina lacks introduced animals but has a very limited area of humid-zone vegetation, and the rail population is small (see Results); and Pinta is free of introduced mammalian predators, and the goat population has been reduced to fewer than 20 individuals (L. Calvopiña, pers. comm.). However, goats that are still present threaten the rail population.

Franklin et al. (1979) believed the Santa Cruz Galápagos rail population to be fairly stable and not threatened in the foreseeable future. Because of the introduced herbivores and potential mammalian predators, they recommended that the status of the rail be reviewed throughout its range. A census was made of this species on six of the seven islands where it was known to occur; Pinta was excluded for logistical reasons. The relative abundances of the rail were compared among islands and the apparent avoidance of areas with low vegetation was demonstrated. It appears that the rarity of the San Cristóbal and possibly the Floreana populations and the restricted area of occurrence on Santiago were due to extensive grazing by introduced herbivores, chiefly goats, cattle, and horses, which reduced suitable habitat and possibly increased predation. Management recommendations are made that may be necessary to increase population levels, thereby reducing the rails' chance of early local extinction.

Overview of the Habits and Habitats of the Galapagos Rail

The rail has been studied most extensively by Franklin et al. (1979) in the highlands of Santa Cruz. They found rails occurring in the farms and all of the highland vegetation zones. Their work showed it to be largely insectivorous, taking primarily small invertebrates. The Galápagos rail appears to be monogamous and territorial and builds semidomed ground nests in dense vegetation. They also found incubation to be relatively long, lasting about 23–25 days. The Galápagos rail is loath to fly, and when seen, it travels through runways it makes in the herbaceous vegetation.

Methods

Rails were censused using playback recordings of the territorial call of the Galápagos rail recorded on Santa Cruz by A. Franklin and deposited in the Library of Natural Sounds at Cornell University. Calls were played for 15 seconds in each of four 90° directions from a Sony TCS-450 recorder, hand held approximately 1.5 m from ground height. Vocal responses from rails were counted during the one-minute playback period and for two minutes following the end of the playback. Birds responding within an estimated 25-m radius (0.20-ha circular plot) were counted; only responses that were clearly from different birds were included. Therefore, density estimates of responding birds were probably lower than actual occurrence. Such a method likely reduces bias in relative abundance measures, as rails may call more frequently at higher densities (see Glahn, 1974, for *Porzana carolina* and *Rallus limicola*). Rails were censused at 100-m intervals, except on the southeastern rim of Fernandina and in several areas on Isabela, San Cristóbal, and Floreana, where they were censused at 50-m intervals in order to census more effectively rails in areas of restricted habitat. Vegetation type was recorded in 25% units for each 0.20-ha circular plot, except for the farm zone of Santa Cruz, where vegetation type was noted in the area of responding rails. Vegetation was classified in the tall herbaceous height class if the plot contained at least 25% cover greater than 30 cm tall. If the plot had less than 25% cover by tall herbs and greater than 25% cover by low herbs ($\leq$ 30 cm tall) it was included in the low herbaceous height class.

The term "density" refers to the number of calling rails during the three-minute playback–listening period. Density, as expressed per ha, is the number of calling rails in five 0.20-ha circular plots. The rail density for Pozo Colorado is based on the total number of rails heard in the wet area (ca. 1 ha).

SANTA CRUZ

Fourteen farms were randomly selected from a list of all farms greater than 20 ha (N = 151) on Santa Cruz. For each farm four–six 500-m transects were randomly located using a grid system on a map of the farm zone made by Ingala (Instituto Nacional Galápagos). Rails were censused in the farm zone from 16 September to 1 October 1986. In the highlands of Santa Cruz within the Galápagos National Park (GNP), a 4.5-km transect beginning about 1.3 km south of Media Luna to about 0.8 km north of Puntudo was established. Data analysis reported for Santa Cruz (GNP) includes eight censuses made from 16 October 1986 to 5 March 1987. Territorial calls were heard throughout this period without any apparent seasonal trends in frequency of response.

OTHER ISLANDS

The other islands were censused in a similar fashion, although each transect was only censused once. Rails were censused in areas previously reported to have had rails or that appeared as suitable habitat. Santiago was censused from 21–26 November 1986; Floreana, 19–25 January 1987; San Cristóbal, 28 January–1 February 1987; Isabela, 6–11 February 1987; and Fernandina, 5–6 April 1987.

STUDY SITES

On Santa Cruz, the sampled farm zone was primarily composed of introduced elephant grass (*Pennisetum purpureum*) pastures, introduced guayava (*Psidium guajava*) shrub patches, and a mixture of herbaceous plant pastures and scattered forests, primarily cedar (*Cedrela odorata*) and avocado (*Persea americana*). Almost the entire southern highlands of Santa Cruz have been altered by agricultural interests. The transects in the GNP on Santa Cruz were located in *Miconia*, fern, and herbaceous meadow areas.

On Floreana, rails were censused throughout the farm zone (similar vegetation as on Santa Cruz) and in the GNP highland areas. Guayava forests with a fern understory were most common in the GNP areas censused. Several areas were open and mesic with sedges and other herbs. On Santiago, rails were censused in the guayavillo (*Psidium galapagensis*) forests near the southern summit and in meadow areas at the plateau of La Central. The high northern section of Santiago ("Jaboncillo") was surveyed, listening for calls without using tape recordings. On San Cristóbal, rails were censused in the farm region of El Chino and the upper plateau in the region of San Joaquin and El Junco. The plateau area was primarily pasture and short, dense, guayava shrubs. On Isabela, rails were censused in the grass–fern area on the southeastern slope of Sierra Negra, including Pozo Colorado, a small (ca. 1 ha) wet area. At Pozo Colorado, rails were censused at 50-m intervals. The census was extended to 500 m from the center of the wet area to the west and east, and ca. 1 km to the north and south. During 1985 a large area of Sierra Negra was burned; data reported here do not come from sites that had evidence of burning. I censused the southeastern rim and southwest slope of Fernandina in densely vegetated areas with herbaceous cover. Hamann (1981) described floristics for most of the areas in the study sites.

TABLE 1. Numbers of 0.20–ha circular plots with 0, 1, 2, or >2 rails responding to tape recordings on 12 sites on 6 islands, Galápagos, 1986–1987.

Islands Sites	Elevation (m)	Numbers of rails per plot 0	1	2	>2	Total plots
Santa Cruz						
Farm zone	120–455	314(96.6)[1]	10(3.1)	1(0.3)	0(0)	325
Highlands (Galápagos National Park)[2]	490–700	196(64.3)	90(29.5)	19(6.2)	0(0)	305
Isabela[3]						
Southeastern Sierra Negra	950–1,060	26(57.8)	15(33.3)	4(8.9)	0(0)	45
Northeastern Sierra Negra	810–1,020	14(93.3)	1(6.7)	0(0)	0(0)	15
Poza Colorado	590–630	45(91.8)	3(6.1)	1(2.1)	0(0)	49
Fernandina						
Southeastern rim	1,330	29(100)	0(0)	0(0)	0(0)	29
South-southwestern slope[4]	800	—	—	—	—	
Santiago (southern highlands)						
Wooded areas	480–600	43(100)	0(0)	0(0)	0(0)	43
Herbaceous meadows	580–660	59(84.3)	7(10.0)	2(2.9)	2(2.9)	70
San Cristóbal						
Upper plateau	400–650	78(100)	0(0)	0(0)	0(0)	78
El Chino	130–230	23(95.8)	1(4.2)	0(0)	0(0)	24
Floreana						
Highlands	230–480	150(100)	0(0)	0(0)	0(0)	150

[1]Percent of total plots for each site.
[2]Includes all plots in the replicated censuses (October 1986–March 1987).
[3]Nonburned sites.
[4]Area not systematically censused; free-calling rails found.

RESULTS

SANTA CRUZ

Rails were found in the farm zone from 125 m to 445 m elevation. Although rails were more often found in higher-elevation plots, the difference between the mean elevation of plots with rail response and without was not significant in the farm zone (Wilcoxon test, $P > 0.10$). Rails were found in a variety of vegetation types, occurring in wooded areas as well as in tall herbaceous pastures. They were not found in low height class pastures, although a small number of plots occurred in this height class (N = 21, 6.4% of total number of plots). Based on this number of plots and the low number of rails located, they would not have been expected to have been found in the low height class pastures if they were distributed randomly among vegetation classes. Rail density was low throughout the farm zone (Tables 1, 2) and tended to be lower than other sites when densities of playback areas with rails were compared (Table 2). However, densities in plots where rails were found were similar among islands and sites ($X^2 = 3.4$, $P > 0.3$). Density of responding rails was greatest in the higher elevations of the GNP and varied among census days with a mean of 2.1 rails/ha (Table 2). Density increased with increasing elevation ($r_s = 0.92$, $P < 0.005$; Fig. 1). The plot with the highest elevation (695 m) had a mean density of 5.2 rails/ha.

ISABELA

Excluding burned sites, rail density was slightly higher on southeastern Sierra Negra than on Santa Cruz (Table 2). There was no difference in the frequency of rails responding in playback areas

TABLE 2. Densities ($\bar{X} \pm SE$) of responding rails during playbacks among selected islands, Galápagos, 1986–1987.

Islands Sites	Rails/ha All plots	Rails/ha Plots with rails responding
Santa Cruz		
Farm zone	0.18 ± 0.05	5.45 ± 0.45
Highlands (Galápagos National Park)	2.10 ± 0.19	6.65 ± 0.55
Isabela		
Sierra Negra (SE)	2.45 ± 0.50	6.05 ± 0.50
Poza Colorado	—[1]	4.00[1]
Santiago		
Southern highlands	—[2]	8.50 ± 1.65

[1]Density reported for entire area (see Methods).
[2]Not reported due to large area censused and the patchy rail distribution (see Results).

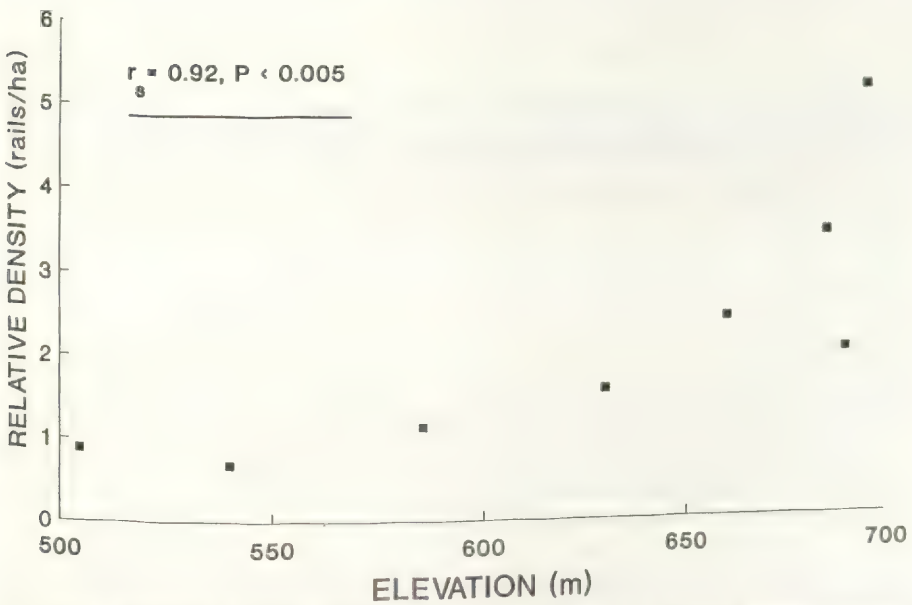

FIGURE 1. Relationship of relative density of responding Galápagos rails to elevation, southern highlands (GNP), Santa Cruz Island, Galápagos, October 1986–March 1987.

with 100% cover of tall vegetation and playback areas with 25–50% low herbs (Fisher's exact probability test, $P > 0.40$). All nonburned playback areas had greater than 50% tall herbaceous cover. Fourteen horses were seen in the eastern portion of the upper area of Sierra Negra; they may have been responsible for the patchy areas of low herb cover that appeared grazed.

At Pozo Colorado, four rails responded in the wet areas (approximately 1 ha) and none were observed greater than 300 m from this area. Evidence of herbivore grazing was found throughout the area; however, a mixture of tall and short herbs remained.

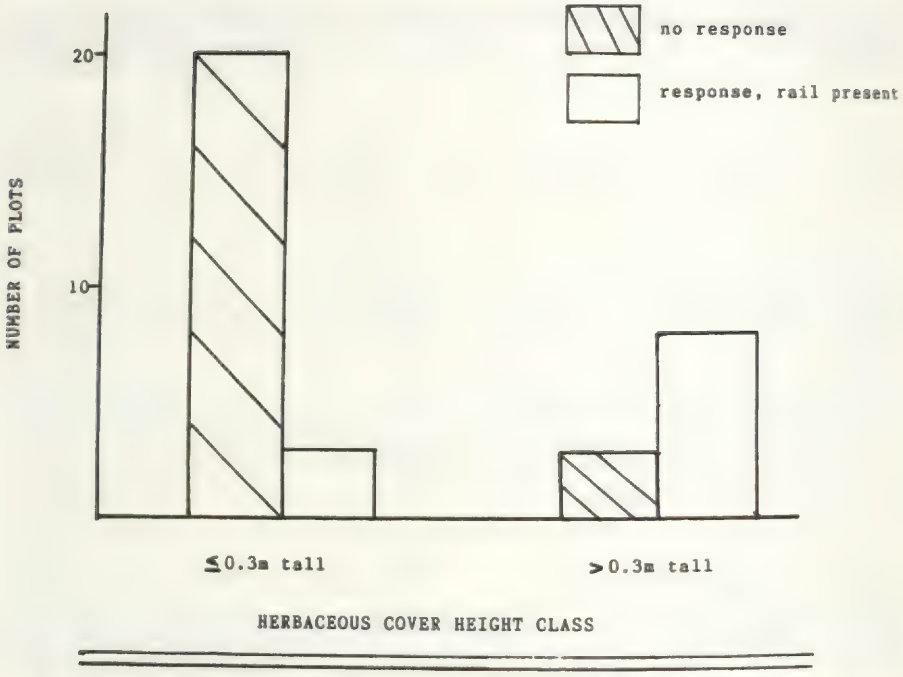

FIGURE 2. Comparison of Galápagos rail presence with herbaceous vegetation height class, Santiago Island, Galápagos, November 1986. There may be two-way interaction with the presence of a freshwater pool and height class. In this figure, only plots with a freshwater pool are included. Rail presence between the height classes was nonrandom (Fisher's exact probability test, $P = 0.001$), with a higher proportion occurring in the taller herb cover.

FERNANDINA

Rails were found at 800 m elevation on the south–southwest slope where grasses were abundant. They were not found on the southeast side of the rim (1,330 m), where tall grasses and sedges were also abundant (Table 1). T. de Roy (pers. comm.) found rails at about 800 m more frequently than at the rim's southeastern side during several trips to Fernandina. The number of rails appeared to be small, and they are perhaps scattered among suitable sites.

SANTIAGO

Rails were found only on the southern highlands of Santiago at an elevation of 550–650 m (Table 1). Rails were found at 11 playback areas; density of responding rails in sectors with rails was higher than on other islands (Table 2). Two of these plots had three or four rails responding during the playback period, respectively (Table 1). A total of 25 responding rails were recorded during the playbacks and while walking between transects.

Rails were found more often than expected in playback areas with a freshwater pool present than in playback areas without pools under the model of equal distribution among classes (Fisher's exact probability test, $P = 0.0004$). Similarly, rails were found more often than expected in playback areas with pools and greater than 25% tall herbaceous cover than in areas with pools and low herbaceous cover (Fisher's exact probability test, $P = 0.001$, Fig. 2). Many sites in the low herb

class were extensively grazed and had 100% cover of herbs less than 30 cm tall. There may be a two-way interaction with the presence of a pool and vegetation height; however, this question was not possible to examine because of a small sample size (N = 11).

SAN CRISTOBAL

Only one rail was found on San Cristóbal, in the farming area of El Chino at 200 m elevation. Despite intensive and extensive searching, rails were not found in the higher elevations (Table 1). The herbaceous vegetation was characteristically low and heavily grazed by cattle and horses, especially near the numerous freshwater pools.

FLOREANA

Several areas appeared as suitable rail habitat on Floreana. Yet the Galápagos rail was not found despite seven days of searching (Table 1). At the base of several hills there were freshwater pools with tall, dense herbaceous vegetation. In all areas that appeared suitable there were numerous signs of feral pigs.

Discussion

Rail density increased with elevation on Isabela and Santa Cruz, probably because of the greater moisture in the higher zones. This is supported by the findings on Fernandina where rails were found only in the more humid area of 800 m elevation rather than at the rim (1,330 m), which is above the cloud belt (Hamann, 1981). The apparent absence of rails away from the wet area at Pozo Colorado (Isabela) also indicates the propensity of the rails for mesic areas. Although they are scarce, the presence of rails at 200 m elevation on San Cristóbal and the absence or rarity of rails in the higher zone (550–600 m) is unlikely to be characteristic of their normal distribution and abundance. The upper zone of San Cristóbal, unlike much of Isabela and Santa Cruz, is almost exclusively private land and is used heavily as pasture for domestic cattle and horses. Although there are areas of pasture with herbaceous vegetation greater than 30 cm tall, they are scattered among a larger framework of short grazed herbs. The upper area of San Cristóbal receives heavy precipitation, and for a given altitude, receives more rain than Santa Cruz and Isabela (see Hamann, 1979b). It is the only island with permanent freshwater streams and has numerous small depressions that form freshwater pools. Itow & Weber (1974) found bogs only on San Cristóbal, Santiago, Santa Cruz, and southern Isabela, and commented that the bogs of San Cristóbal were (p. 46) "heavily disturbed by free ranging cattle." San Cristóbal probably once had a very large rail population. Few early explorations were made on San Cristóbal early in the 19th century, hence our knowledge of early distributions and abundance of birds is poorly known prior to habitat destruction by humans (Grant, 1986).

Santiago also presents a similar situation. During the census, rails were restricted to a few areas on the upper plateau. The total population of rails may number fewer than 100. Darwin (1896, p. 376) noted "great numbers of a very small water-rail" in the upper part of Santiago. It is easy to picture the highland region having had a large rail population. The number of goats is now very high, so why several areas still retain a dense herbaceous vegetation when neighboring areas are extensively grazed remains an enigma. It is interesting that the density of rails in playback areas where rails were recorded tended to be higher than in the other islands I censused. This may be due to excellent habitat (albeit restricted in size) or to a changed structure within the population due to the restricted opportunities for successful dispersal. A higher proportion of young birds may remain at their natal site.

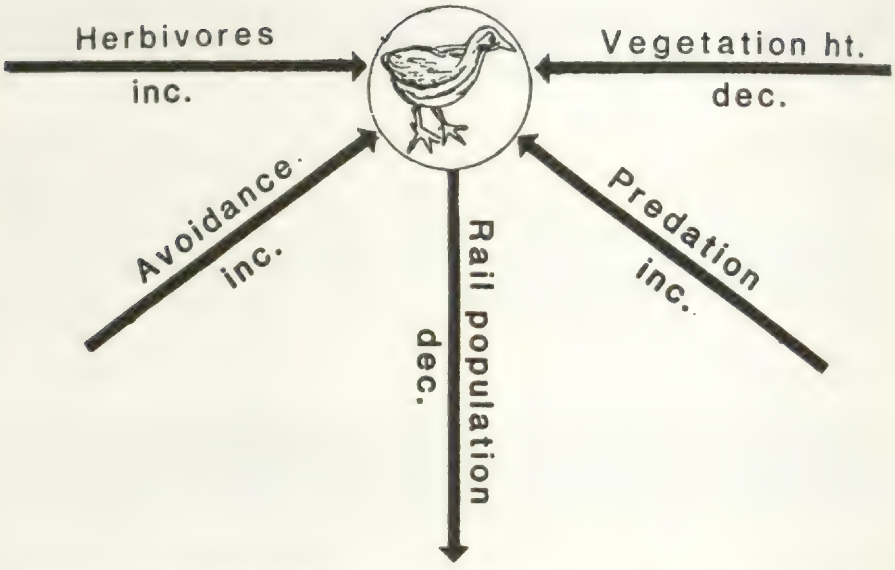

FIGURE 3. Herbivore–predator model. As the number of herbivores increases, there is likely to be an increase in the patchiness of low and tall herbs, with an overall decrease in the proportion of tall herbs. This model predicts that as areas of tall cover decrease and the cover height patchiness increases, the rail population will decline by increased predation and a decline of suitable habitat.

The rail was rare or extirpated on Floreana. There appeared to be suitable habitat for it. The plateau area of the highlands is no greater than 360 m elevation, and rainfall there appears to be lower than on the other islands censused (Hamann, 1979b). Thus it is likely that there has never been a large population of rails. Feral mammals, which have had a long history on Floreana (Darwin, 1896; F. Cruz, pers. comm.), may be responsible for the present status of the Floreana rail population. Although the rail may be present, F. Cruz (pers. comm.) has not seen this species on Floreana since 1983. The drought during 1985 was severe, perhaps restricting this species to fewer sites, thereby increasing the possibility of extirpation. Floreana has the largest number of recent vertebrate extinctions (see Steadman, 1986), which is probably a result of the early history of feral mammals.

Grazing by goats on Pinta appeared to reduce the population of rails (see Franklin et al., 1979). With the reduction of goats in the early 1970s, the rails appear to have recovered (see Franklin et al., 1979). During 1978, rails were very common (P. Grant, pers. comm.). However, the population is vulnerable to declines as long as goats remain.

Rails appear to avoid areas with herbaceous ground cover of short herbs. Avoidance is likely to be augmented by selective pressures by indigenous (e.g., barn owl, *Tyto alba* (de Groot, 1983)) and introduced predators (e.g., feral pigs (Coblentz & Baber, 1984)). When the density of herbivores increases, the herbaceous vegetation would probably become more patchy, with an increase in areas with low herbs. Predation may be facilitated in such an environment. Rail populations may decline if areas of low herb cover are avoided and may also decline by an increase in predation in patchy areas (Fig. 3).

MANAGEMENT RECOMMENDATIONS

It is clear that several rail populations are threatened. If the populations of rails on Santiago and San Cristóbal remain small, early extinction (as Floreana may have experienced) is more likely due

to natural disturbances, inbreeding (see Schonewald-Cox et al., 1983), and population changes of predators/herbivores. Optimally, the goat and pig populations need to be eliminated on Santiago. Due to the large size of the highland region and humid conditions, Santiago could potentially provide a reserve for this species. The problem on San Cristóbal is more difficult. Acquisition of areas of the plateau region and exclusion of herbivores would be necessary. The size and shape of the reserve must minimize the area exposed to grazed areas, thus minimizing the influence of predators. Domestic animals must not be permitted to roam free on Floreana. Wild pigs were once eliminated (F. Cruz, pers. comm.); however, they have been reintroduced from domestic stock. The area of Cerro Narranjo and other wet areas that form at the base of several hills would be the best sites for fencing if herbivores cannot be excluded from the park. The few remaining goats on Pinta must be eliminated to reduce the major threat to that population.

Protecting areas from herbivores would also promote plant conservation. Restoring natural vegetation and protecting existing areas should concurrently help the rail populations. Thus, joint conservation efforts are needed. I strongly suggest a plan of action to restore the plant communities of Santiago, the only uninhabited island with a large highland region. Eradication of introduced herbivores on the important island of Santiago would be a major ecological success story.

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PLANT–ANIMAL INTERACTIONS: CONSUMPTION OF SEEDS BY DARWIN'S FINCHES[1]

P. R. Grant and B. R. Grant[2]

Abstract

Studies of the behavior and ecology of Darwin's Finches involve identifying their foods and estimating their food supply. Many of the foods are fruits and seeds, especially for the ground finches (*Geospiza* species). Estimating seed abundances is made difficult by strong patchiness in their distributions. A large sampling program is required to minimize these difficulties: large numbers of randomly chosen samples from a specified area are needed. This in turn requires much effort that detracts from the study of the finches themselves. The sampling program we have used is a compromise. It enables us to detect large changes in the abundance of individual seed species through time and large differences in abundance between sites on different islands. Repeated sampling has been carried out twice a year on Isla Daphne Major since 1976, and less consistently on Isla Genovesa since 1978. Year-to-year variation in seed densities is pronounced and strongly correlated with rainfall. In drought years, such as 1977, little seed production occurs, and seed densities fall as a result of consumption by finches and other animals, including doves. In very wet years seed production is greatly enhanced, and seed densities remain high well after the rains have ceased because they greatly exceed the needs of the granivores. In 1983, the year of an exceptionally strong El Niño event, overall seed density increased to a level three orders of magnitude higher than in the drought of 1977. Fluctuations in seed abundance and composition have a strong influence on the sizes of Darwin's Finch populations and the composition of finch communities on each island. As a model for investigating interactions between other granivorous species of animals and their food supply, these studies could be improved by using seed traps to measure seed production. Sampling the aboveground vegetation and the production, consumption, and dispersal of seeds should form the basis of the ecological study of natural plant populations on the Galápagos.

A natural community of organisms is structured by its component members, and it functions according to the interactions among those members. The highly diverse interactions between plants and animals are only one class among many interactions. Plant–animal interactions include the dispersal of seeds by animals, effects of animals upon plant production, limitation of animal population size by plant food supply, diets of animals determined by plants, pollination of plants by animals, and many others. In our studies of Darwin's Finches we have examined the determination of finch diets and population sizes by plant food supply (Grant, 1986a). The results should be of general interest because there are no other comparable studies in the Galápagos, and there are important lessons for plant ecology on the Galápagos to be learned from them.

The Study of Finches

Our studies began in 1973 with an attempt to determine if interspecific competition for food had been an important factor in the evolution of Darwin's Finches, as Lack (1947) had argued. To

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answer this question we needed to know, quantitatively, the diets of the species. Diets can be determined by either watching birds feed and recording what they eat, or by examining the contents of their stomachs obtained with the aid of an emetic or from dead specimens. These observations show what birds eat, but to find out why they choose particular food items it is necessary to establish what is available to them. We attempted to do both things, to characterize diets and food supply.

Thirteen species of Darwin's Finches live on the Galápagos. Six are ground finches (*Geospiza* spp.), six are tree finches (*Camarhynchus, Cactospiza,* and *Platyspiza* spp.), and one is a warbler finch (*Certhidea olivacea*). From stomach content analysis Bowman (1961) established that the ground finches are basically granivorous, although they do eat anthropods such as caterpillars; the tree finches are basically insectivorous, with the exception of the vegetarian finch (*Platyspiza crassirostris*); and the warbler finch feeds almost entirely on arthropods. It is much easier to determine the abundance and identity of plants than it is to do the same for arthropods, and for this reason we restricted our attention to the ground finches.

Estimating Plant and Seed Abundance

At each of eight lowland sites on seven islands we set up a study site in a representative piece of habitat (Abbott et al., 1977). We surveyed an area of about 23,000 m^2 and marked the coordinates of a grid of 10 m $\times$ 10 m units with flagging. The next step was to choose 50 1-m^2 quadrats with the aid of a random numbers table and to mark the edges of each quadrat with string. We then estimated the percentage cover of each species of living plant, counted the number of fruits and seeds attached to each plant species, and counted the number of fruits and seeds on the ground and the surface layer of the soil to a depth of 2 cm in two 0.1-m^2 areas of the quadrat. We identified seeds and fruits with the help of Wiggins & Porter's (1971) *Flora of the Galápagos Islands* and measured 20 specimens of each species. This random sampling program enabled us to obtain unbiased estimates of the abundance of each species of seed and fruit.

These studies were conducted from February to June 1973. Rainfall had been heavy in January of that year, and almost no rain fell at lowland sites thereafter. Thus the study was conducted in the early part of the dry season, when finch breeding was declining or had ceased altogether. To compare seed abundance in early and late times in the dry season we returned in November 1973, revisited four study sites, added a new one, and repeated the sampling.

To establish the extent of annual variation in seed supply we have repeatedly sampled the study site on Isla Daphne Major (Boag & Grant, 1984a; Gibbs & Grant, 1987a, b), and less frequently resampled the same study site on Isla Genovesa (Grant & Grant, 1980, 1987). Many other islands have been investigated, and seed sampling has been carried out at two or more sites on five of the islands (Schluter, 1982a, b; Schluter & Grant, 1982, 1984): Santiago (2 sites), Marchena (2), Española (3), Fernandina (4), and Pinta (6). The six sites on Pinta were established at approximately uniform intervals along an altitudinal transect from near the coast to just below the summit.

Some changes were made to the methods, such as reducing from 0.1 m^2 to 0.0625 m^2 the areas on the ground in which all seeds were counted, but these changes were minor.

Estimating Finch Numbers and Diets

On Daphne Major we have been able to band and mark individually virtually all birds on the island, so finch numbers have been determined by direct counting. On Genovesa almost all finches have been banded each year of a 10-year study in an area that constitutes about 10% of the island. Direct counting has provided us with a measure of finch abundance there. On all other islands finch numbers have been estimated by mist-netting. Two or three nets were opened at dawn and closed two to three hours later. They were opened once more in the next two days, and then used in a new

TABLE 1. Numbers of seeds and fruits on the principal plant species in the quadrats on Isla Genovesa, expressed as mean number per $m^2 \pm 1$ standard error. Compare the abundance in the very wet year of 1983 with the paucity in the subsequent dry years and the dry season (November) of a normal year (1978). Seeds of three species known to be abundant in 1983 but not counted were indicated by the word "Many." *Waltheria ovata* is omitted from the table because it scarcely ever produces seeds.

	1978 March	1978 November	1983 July	1984 July	1985 July
Corida lutea	5.9 ± 3.9	1.8 ± 0.6	0	0.5 ± 0.1	1.2 ± 0.4
Croton scouleri	9.4 ± 2.7	0	15.7 ± 5.3	0	0
Bursera graveolens	7.7 ± 2.8	0	0	1.2 ± 0.5	0
Opuntia helleri	1.7 ± 0.8	1.6 ± 0.6	0.5 ± 0.1	0	0
Lantana peduncularis	38.7 ± 29.0	0	9.0 ± 2.8	0	0
Heliotropium angiospermum	0	0	37.8 ± 13.3	0	0
Sida salviifolia	0	0	Many	0	0
Cacabus miersii	0	0	Many	0	0
Ipomoea linearifolia	0.5 ± 0.3	2.2 ± 1.6	0	0	0
Cyperus spp.	0	0	464.0 ± 184.4	0	0.2 ± 0.2
Eragrostis and *Trichoneura* spp.	129.3 ± 124.1	51.7 ± 32.4	Many	0.8 ± 0.4	0

position in the study area. We stopped netting when the total netting effort had lasted for 198 meters × hours. Captured finches were weighed, measured, color-banded, and released unharmed.

Diets were determined by observing and identifying the food item taken by a bird, and doing this for as many birds as possible in mornings only. We first recorded all foods taken in a period of 300 seconds (maximum) of observation of each bird, then changed the method to recording the first identified item seen to be taken by a bird. The change in method allowed us to sample the diets of many more birds.

Changes in Plant and Seed Abundance

Seed and fruit abundance, and the abundance of many of the plants from which they come, vary in time and space. They vary from island to island, from lowlands to highlands on a single island, from wet season to dry season, and from wet years to dry years. Spatial variation has been documented and discussed by Abbott et al. (1977), Smith et al. (1978), Schluter (1982a, b), and Schluter & Grant (1982, 1984). We will concentrate here on temporal variation and use data from our study on Genovesa to illustrate the main points (Grant & Grant, 1989).

Seasonal variation in the abundance of seeds on Genovesa is shown in Table 1. Sampling errors are large because all seed species are patchily distributed, as Boag & Grant (1984a) showed in a more detailed study on Daphne Major. *Croton scouleri* and *Bursera graveolens* seeds were less common in the late dry deason than earlier in the year. It also appears that other seed types had declined in abundance, with the exception of *Opuntia helleri* and *Ipomoea linearifolia*. Seasonal decline in seed abundance is a general phenomenon at lowland sites among islands (Smith et al., 1978; Schluter, 1982a, b).

Annual variation is also shown in Table 1. It can be appreciated most easily by comparing abundances for the month of July. In a normal year the wet season ends on Genovesa in March or April, so July is in the dry season. In 1983, not a normal year, July was the last month of heavy and extensive rainfall associated with an extraordinary El Niño event. Nineteen eighty-four was an unusually dry year, with rainfall amounting to less than 60 mm, and in 1985 no rain fell at all. The contrast in seed abundance between the wet year of 1983 and the dry year of 1985 could not be greater. With the exception of *Cordia lutea*, seed abundances were far higher in 1983 than in the

TABLE 2. Mean percent cover of plant species in 50 random quadrats of 1 m^2 each in a study area on the south side of Isla Genovesa. Nineteen seventy-eight was a normal year, 1983 was exceptionally wet, and in 1985 there was a drought. Compare the stability of *Bursera* and *Opuntia* with the fluctuations of *Cordia*, *Croton*, and others. One standard error is given with each mean.

	1978 March	1983 July	1985 July
Cordia lutea	5.5 ± 1.8	29.2 ± 3.8	18.3 ± 4.3
Croton scouleri	13.2 ± 2.8	33.1 ± 3.9	6.6 ± 1.6
Bursera graveolens	11.4 ± 2.3	15.4 ± 2.5	14.3 ± 3.1
Opuntia helleri	10.1 ± 3.6	11.0 ± 2.3	15.9 ± 4.4
Lantana peduncularis	1.2 ± 0.8	11.4 ± 1.5	0.0
Waltheria ovata	0.5 ± 0.2	5.1 ± 2.9	1.7 ± 1.1
Heliotropium angiospermum	0.0	8.2 ± 3.7	0.0
Sida salviifolia	0.0	2.1 ± 2.0	0.0
Cacabus miersii	0.1 ± 0.1	5.3 ± 1.3	0.0
Ipomoea linearifolia	0.1 ± 0.1	0.0	0.0
Ipomoea habeliana	0.0	1.9 ± 0.3	0.1 ± 0.1
Cyperus spp.	0.0	3.9 ± 1.0	0.0
Eragrostis and *Trichoneura* spp.	0.2 ± 0.1	2.4 ± 0.3	0.0

TABLE 3. Frequency of occurrence of plant species (%) in 50 random quadrats of 1 m^2; x = presence elsewhere in the study area. Further details of the study area and methods are given in Grant & Grant (1980).

	March 1973	November 1973	March 1978	November 1978	July 1983
Cryptocarpus pyriformis	x	x	4	x	x
Cordia lutea	36	34	40	38	42
Heliotropium angiospermum	x	x	x	x	22
Ipomoea habeliana	4	x	x	2	2
Ipomoea linearifolia	2	2	2	x	x
Merremia aegyptica	x	x	—	—	x
Cacabus miersii	x	x	2	—	4
Lantana peduncularis	8	x	4	2	26
Bursera graveolens	58	58	66	68	42
Opuntia helleri	8	6	20	20	16
Chamaesyce amplexicaulis	2	x	x	x	x
Chamaesyce recurva	4	x	2	2	2
Chamaesyce viminea	x	x	x	x	2
Croton scouleri	44	68	56	58	68
Abutilon depauperatum	4	x	2	—	x
Portulaca howellii	x	x	x	x	x
Waltheria ovata	6	16	6	8	14
Cyperus spp.	x	x	x	x	18
Eragrostis spp.	16	2	—	—	2
Trichoneura lindleyana	4	—	—	—	8
Sida salviifolia	—	—	—	—	4

wet season of a normal year (1978). On Daphne Major seed density was three orders of magnitude higher in 1983 than in the drought of 1977 (Boag & Grant, 1984a; Gibbs & Grant, 1987b).

Tables 2 and 3 provide different measures of the frequency of occurrence of different plant species in the study area under contrasting conditions. The main point to notice is that long-lived

perennial species like *Bursera graveolens* and *Opuntia helleri* remain relatively constant, whereas some of the annuals and short-lived perennial species like *Cyperus* sedges and *Heliotropium angiospermum* fluctuate substantially in occurrence. Vegetative growth was extensive in the very wet year of 1983, and the vegetation in general became much thicker. This is reflected in the fact that the percent cover of species like *Cordia lutea* and *Croton scouleri* rose to unprecedented levels in 1983 (Table 2); the difference between mean percent cover values in 1978 and 1983 is highly significant in each case ($P < 0.001$), as shown by *t*-tests with arcsin-transformed data. On the other hand, their frequency of occurrence remained essentially unchanged (Table 3). Thus, where they occurred they grew thicker, either mainly due to vegetative growth (*Cordia lutea*) or mainly due to germination of seeds and the production of new plants (*Croton scouleri*), but they did not spread much into unoccupied places.

Together the data show the basically unchanged nature of the plant community composition over a 10-year period, with fluctuations in the fortunes of those species most sensitive to levels of rainfall. The data are important because they come from undisturbed habitat; the island has not been settled by humans, and there are no exotic or alien species of plants or animals on the island.

Two extra features that are not reflected in the data need comment. The first is that the growth of vines, particularly *Merremia aegyptica* and *Ipomoea habeliana*, varies enormously from year to year. Their prolific growth in 1983 is illustrated in Grant (1986a). If any plants could be called El Niño plants these, and *Cacabus miersii*, would be strong candidates. The second point is that no new species of plant sprang forth from seeds in 1983, having lain dormant since the last El Niño event. Seeds of *Erythrina velutina* germinated only in 1983, but the species is not new to the island; a single tree has been present for the duration of our study, and probably for decades longer.

Changes in Finch Diets and Numbers

Finches eat seeds and fruits and cause the supply of this food type to decline from the end of one wet season to the beginning of the next. On some islands other organisms, including native rats, contribute to the decline. As food supply declines during the dry season, the diets of different finch species diverge. At times of food scarcity each finch species feeds most on the foods it is best able to deal with by virtue of the size and shape of its beak. We have seen this pattern repeatedly, most conspicuously on the two islands we have visited most often, Daphne Major and Genovesa (Smith et al., 1978; Grant & Grant, 1980; Schluter, 1982a; Boag & Grant, 1984b; Price, 1987).

In the dry season finch population sizes are correlated with the amount of seeds and fruits available (Grant, 1986b). At this time of the year total ground finch biomass was positively correlated with seed biomass among seven islands ($r = 0.962$, $P < 0.01$), as well as among six sites along an altitudinal transect on Pinta ($r = 0.966$, $P < 0.01$). On Daphne Major, during a very long period of dryness due to the near absence of rain in 1977, finch biomass and seed biomass declined in a correlated manner ($r = 0.921$, $P < 0.05$). Finch mortality varies in proportion to the amount of food that is available. Mortality is high when seed supply is low, and low when seeds are abundant. Thus on Daphne Major, mortality rates of *G. fortis* and *G. scandens* were inversely related to seed abundance ($r = 0.5$, $P < 0.05$ in each case), during the period 1976–1983 (Gibbs & Grant, 1987a). These correlations provide strong, although indirect, evidence that finch population sizes are limited by seed supply. Experimental studies would be needed for a more rigorous assessment of cause and effect (see Grant, 1986b).

In addition to these ecological effects, food supply has evolutionary effects upon finches. These evolutionary effects have been established by following the fates of known and measured birds through stressful periods of drought and a declining food supply, and documenting which birds die and which ones survive. Under these conditions on Daphne Major, large birds in the population of medium ground finches (*Geospiza fortis*) survive better than small birds (Boag & Grant, 1981; Price et al., 1984). They do so because as seed supply declines small seeds become particularly scarce.

so finches must turn increasingly to the proportionately more common large and hard seeds, and only the large finches with large beaks are able to crack these seeds and extract the kernels. Thus large size is favored by natural selection, and we refer to this as evolution because we know there is a large amount of genetic variation associated with the observed size variation (Boag, 1983). A better term would be microevolution, because the amount of change in beak and body size caused by differential survival is no more than a few percent, but it is real and clearly demonstrated statistically (Boag & Grant, 1981; Price et al., 1984).

Discussion

In the last 14 years we have learned much about how the ground finches are influenced by changes in their food supply. We remain largely ignorant, however, of how particular plant species are influenced by the finches, or other consumers, and how tree finches and the warbler finch interact with their food supply. With regard to the other interactions mentioned in the introductory paragraphs, very little is known about the dispersal of seeds by finches, or by any other animals, and their subsequent germination (e.g., see Rick, 1966; Grant et al., 1975, 1976), and the same is true of the pollination of flowers by finches and insects (e.g., Linsley, 1966; Grant & Grant, 1981; McMullen, 1985, 1986). This can be taken as a cause for concern (how can we be so ignorant?) or as a cause for excitement (there is much that can be learned).

We would like to emphasize three lessons to be learned from the studies of Darwin's Finches and their food supply. The first is the desirability of long-term field studies. Elsewhere in the world it is becoming increasingly realized that for many ecological questions long-term studies are needed to encompass the full range of environmental conditions experienced by the organisms of interest (e.g., see Strayer, 1986). Extreme conditions may have an influence on organisms out of all proportion to their rarity (Wiens, 1977). On Galápagos this should be self-evident; we have recently witnessed an extraordinary annual variation in rainfall, ranging from the probable maximum for the century (Grant, 1984) to drought conditions a mere two years later. Unfortunately, as the contributions to the chronicle of El Niño on Galápagos make clear (Robinson & del Pino, 1985), the effects of such variation on plant communities passed almost unmeasured and unrecorded, with few notable exceptions (Grant & Grant, 1985; Hamann, 1985). This is a great pity, because a golden opportunity was missed to establish a base line of normal and extranormal plant population fluctuations against which to measure the effects of anthropogenic disturbance. Long-term monitoring of plant populations is needed.

The second lesson is similar; there is a need to estimate seed and fruit production. In our studies we did not measure production of seeds and fruits because of lack of time. Instead we measured standing crops of seeds and fruits at two or more times a year. These may not be a reliable index to the amount of food produced and hence available to the finches over a period of time if different seed types are produced at different rates and/or they are depleted by the finches at different rates. With more time we would have used seed traps to measure production directly; we would have had to design different types of traps for the different types of seeds falling from structurally different plants. This gap in our knowledge has pinpointed a general deficiency; there are no seed- and fruit-production values for any plant species in the Galápagos archipelago.

The third lesson emerges from our sampling program. A standard dilemma confronted by an ecologist is whether to study a few individuals (or populations) well, or many less well. A few can be studied with great precision, but they may not be truly representative, in which case they give no reliable information about the population, community, or habitat as a whole. But the opposite research tactic of studying many relatively superficially runs a different risk; it is the risk of no clear conclusions being drawn because the sampling program is not sufficiently intensive and the confidence limits on each estimate are too large for the estimates to have much value, even though they are representative of the whole.

In our seed sampling program we sampled 50 times, randomly, from a large area. The results showed us that confidence limits on our estimates of seed abundance were regrettably large. When we compared estimates of the abundance of the same seed species or plant species at two times we found we were unable to discriminate statistically between them, in some cases, even though the estimated densities differed by a factor of two or more. Yet observing the habitat we were sure there was a real difference in densities. The problem arises from the patchy distribution of most seed types. For the fixed area of our study grid, 50 samples of 1 m^2 each were insufficient. With more time available we would have increased the number of samples by a factor of 10 or more, so increasing both the density of samples as well as the proportion of the total area sampled.

Thus, the final lesson is that the sampling design of a study is crucial to its success. Examining individual plants or quadrats repeatedly gives a description of change, or lack of it (e.g., Hamann, 1979, 1985). Sampling an area with many quadrats over the same period of time provides a quantitative assessment of change, or lack of it, providing the program is well designed, with attention given to the statistical analysis of the results. Perhaps the best strategy, given sufficient time, is to adopt both approaches simultaneously.

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APPENDIX. The plants of Genovesa. The frequency of occurrence of species (%) in 50 random quadrats of 1 m^2 each in a study area on the south side of the island is given in the upper part of the table. x = presence in the study area but not in the quadrats. From Grant & Grant (1980, 1985), with corrections and additions. Three dots (. . .) signify the species was not recorded in the study area.

[1]Species recorded by Wiggins & Porter (1971) or contributors to the official list at the Charles Darwin Research Station but not by us.

[2,3]Species probably brought to the islands by human visitors and recorded in only 1980 ([2]) and 1983 ([3]).

	1978			1983
	January	March	November	July
Cordia lutea	36	40	38	42
Croton scouleri	70	56	58	68
Bursera graveolens	70	66	68	42
Opuntia helleri	26	20	20	16
Lantana peduncularis	4	4	2	26
Waltheria ovata	14	6	8	14
Heliotropium angiospermum	x	x	x	22
Sida salviifolia	. . .	. . .	. . .	4

Cacabus miersii	. . .	2	. . .	4
Ipomoea linearifolia	x	2	x	x
Ipomoea habeliana	2	x	2	2
Merremia aegyptica	. . .	. . .	. . .	x
Cryptocarpus pyriformis	x	4	x	x
Chamaesyce amplexicaulis	2	x	x	x
Chamaesyce recurva	x	x	x	2
Chamaesyce viminea	6	2	2	2
Mentzelia aspera	. . .	x	. . .	. . .
Abutilon depauperatum	. . .	2	. . .	x
Portulaca howellii	x	x	x	x
Cyperus anderssonii	x	x	x	18
Cyperus confertus	x	x	x	
Eragrostis ciliaris	. . .	x	. . .	2
Eragrostis cilianensis	. . .	6	. . .	
Trichoneura lindleyana	4	x	. . .	8

Additional species not present in the study area: *Rhizophora mangle*, *Sesuvium edmonstonei*, *Trianthema portulacastrum*, *Amaranthus sclerantoides*, *Amaranthus squamulatus*, *Mollugo flavescens*, *Mollugo snodgrassii*, *Boerhaavia caribaea*, *Tiquilia fusca*, *Heliotropium curassavicum*, *Pectis tenuifolia*, *Cuscuta acuta*, *Cuscuta gymnocarpa*, *Evolvulus simplex*, *Physalis pubescens*, *Borreria ericifolia*, *Brachycereus nesioticus*, *Chamaesyce abdita*, *Chamaesyce nummularia*[1], *Desmodium decumbens*, *Desmodium procumbens*, *Desmodium canum*, *Ipomoea pes-caprae*, *Erythrina velutina*, *Rhynchosia minima*, *Stylosanthes sympodiales*, *Tribulus cistoides*, *Antephora hermaphrodita*[1], *Aristida repens*[1], *Aristida subspicata*, *Cenchrus platyacanthus*, *Distichlis spicata*, *Panicum fasciculatum*, *Sporobolus virginicus*, *Digitaria horizontalis*[3], *Eleusine indica*[3], *Cassia* sp.[2], and *Polypodium insularum*.

STRATEGIES FOR LIMITING THE INVASION OF PROTECTED AREAS BY INTRODUCED ORGANISMS[1]

I. A. W. Macdonald[2]

ABSTRACT

Using information from the literature, some compiled by the SCOPE Working Group on Introduced Species in Nature Reserves and some from the author's study of the invasion of southern African reserves, general strategies are proposed for limiting the invasion of protected areas by introduced organisms. The strategies embrace: slowing the rate of introduction of new species, reducing the area's susceptibility to invasions, detecting invasions, establishing priorities for management actions, and planning and executing this management. Components of these strategies are illustrated using examples from protected areas around the world. Available information allows an element of prediction in the strategies. This predictive ability along with the systematic approach in the proposed strategies will enable managers to control invasions more readily than in the past.

Introduction of plants, animals, and microorganisms to areas outside their natural distribution ranges has recently been recognized as an environmental problem of global significance. The International Council of Scientific Union's special committee that deals with such matters, SCOPE (Scientific Committee on Problems of the Environment), launched a project in 1982 to address the problem of alien introductions. Entitled *The Ecology of Biological Invasions*, the project has already yielded several national syntheses (e.g., Groves & Burdon, 1986; Kornberg & Williamson, 1986, Macdonald et al., 1986; Mooney & Drake, 1986) and the global synthesis meeting was held in Hawaii in November 1986 (Drake et al., 1989).

The SCOPE project concentrated on introduced species capable of invading untransformed ecosystems (it excluded species invading agricultural fields, plantations, and urban areas). Its findings are particularly relevant to nature conservation authorities whose main responsibility is the maintenance of native communities in untransformed ecosystems. This special relevance was recognized early in the project's formulation by the creation of a Working Group on Introduced Species in Nature Reserves (Anonymous, 1985). As part of the South African contribution to this project (Ferrar & Kruger, 1983) the author was commissioned to investigate the significance of biological invasions for nature conservation in southern Africa (Macdonald, 1983a).

The SCOPE project aimed toward answering three fundamental questions: What makes an introduced species invasive? What makes an ecosystem vulnerable to invasion? How can answers to these questions improve management?

The national contributions produced as part of the project synthesized much current information on these three questions. The significance of invasions for nature conservation has been addressed in the British synthesis (Usher, 1986), in the report of the Nature Reserves Working Group (Brockie et al., 1988; Usher et al., 1988; Loope et al., 1988; Macdonald & Frame, 1988; Macdonald et al., 1988; Usher, 1988), and as part of the global synthesis (Macdonald et al., 1989). Some results

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of the southern African overview have already been presented (Macdonald, 1988b). For simplicity, where possible in the account that follows reference has been made to one of these syntheses rather than to the initial source reference.

The aim of this paper is to draw upon such recent work to present ideas on the improved management of biological invasions in nature reserves. Emphasis is on strategic considerations rather than on techniques. Five areas of strategic management are considered: reducing the rate of introduction of new species, reducing the area's susceptibility to invasion, detecting invasions, establishing priorities for management, and planning and execution of this management.

Slowing the Rate of Introductions

Introductions of new species to a reserve can be intentional or accidental. Most introductions of vertebrates to nature reserves have either been intentional or result from intentional introductions to adjacent areas followed by migration into the reserve. As awareness of the potential problems posed by introductions grows, and as quarantine regulations become more effective, rates of introduction of vertebrate species to nature reserves should decrease, although escapes from the growing international trade in tropical fish species for aquariums (Arthington & Mitchell, 1986) is a major exception. Reserves in tropical and subtropical areas, particularly those with major urban conurbations in their catchment areas, can look forward to a steady stream of new fish species in the years to come (consider the example of Everglades National Park, Florida; Loftus, 1986).

Vascular plants are the only other group where intentional introductions account for a significant fraction of the invasive species in reserves. In the Hluhluwe-Umfolozi Reserve in South Africa, for example, 17 of the 20 invasive woody plant species had been cultivated in staff gardens (Macdonald, 1983b). Similarly, in the Kruger National Park in South Africa the two most important invasive woody plants, *Lantana camara* and *Melia azedarach*, were planted in the park's restcamps (Macdonald, 1988a). *Lantana camara*, a major conservation problem in the Galápagos National Park, likewise traces back to intentional garden introductions (Cruz et al., 1986).

The strategic answer to this unnecessary source of invasive species is to ban the introduction of alien plant species to gardens in a reserve. This is best effected as a ban on species that have not already been present for some time in reserve gardens and that have not shown a tendency to self-seed ("safe" alien species). Phased removal from gardens of all undesirable species should then take place. Wherever possible, species native to the reserve should be used as replacements. Where this is impossible, "safe" alien species should be used (Macdonald, 1983b).

The vast majority of introduced plant species are brought into reserves accidentally (Macdonald, 1988b). Estimates of the rate of successful establishment of such introductions in recent years vary from approximately one to two new species per year for the Jasper Ridge Preserve in Stanford, California (Macdonald et al., 1988), through one new species per year in the Cape of Good Hope Nature Reserve near Cape Town (Macdonald et al., 1987), to one new species every one to four years in a range of subtropical forest and savanna reserves in Natal, South Africa (Macdonald & Jarman, 1985).

Strategic approaches to reducing the rate of accidental introductions are:

1. Limiting tourism within the reserve. This entails limiting visitorship and the extent of infrastructural development within the reserve (Macdonald et al., 1989). In the Prince Edward Islands, which are managed as a nature reserve equivalent to IUCN Category 1 (Scientific/Strict Nature Reserve), Prince Edward Island remains virtually free of introduced species (Watkins & Cooper, 1986), and, not only is tourism prevented, but it has been proposed to minimize research visits to this island (Cooper & Condy, 1988).

2. Limiting the movement of soil into the reserve. Often seeds, fungi (e.g., *Phytophthora cinnamomi;* Shea, 1981), invertebrates (e.g., molluscs and earthworms), and even a few vertebrates (e.g., *Ramphotyphlops braminus;* McLachlan, 1978) arrive in soil.

FIGURE 1. *Lantana camara*, an alien shrub, introduced to Santa Cruz, San Cristóbal, and Floreana, on the latter island representing a serious problem for conservation and rational land use. (Photo taken by O. Hamann).

3. Limiting the movement of vehicular traffic into the reserve. Seeds are often introduced on vehicles (Wace, 1977; Macdonald & Frame, 1988). The occurrence of Argentine ants *(Iridomyrmex humilis)* in the southwestern Cape Province has been shown to be correlated strongly with vehicular access (de Kock, 1984). Boats are notorious for the accidental introduction of rodents to island reserves (Atkinson, 1985), and even airplanes have evidently spread the cane toad *(Bufo marinus)* in northern Australia (Freeland & Martin, 1985).

4. Limiting the movement of plant material into reserves. Thatching grass has been implicated in the introduction of plant species to reserves in Natal (Macdonald & Jarman, 1985) and northern Australia (Macdonald & Frame, 1988). Fodder imports are implicated too. The movement of untreated wood has introduced plant pathogens and several invertebrates (Von Broembsen, 1989; Coaton, 1971; de Kock, 1984).

5. Realigning reserve boundaries to include whole catchments. This helps impede water-dispersed alien species in rivers running into the reserve from transformed and modified outside ecosystems (Macdonald, 1988a, b).

6. Creating "buffer zones" around park boundaries. This is similar to (5) above and is applicable to terrestrial fauna and to animal- and wind-dispersed plants. The optimal width of such a zone will depend on the mean dispersal distance of the alien species involved and the pattern of spread (Auld & Tisdell, 1986; Usher, 1986). Whether the buffer is best located inside vs. outside the reserve depends on factors such as relative ease of access and the relative cost of control measures inside compared with outside the reserve.

7. Creating sharp vegetation discontinuities along the reserve boundary. A barrier to invasion can be established by creating a marked habitat disjunction along the boundary by strategic location of the boundary at the time of reserve proclamation or by vegetation modification (Ambrose, 1986).

Whatever steps are taken to limit introductions, it is almost certain that aliens will continue to arrive, even if at a reduced rate. The next section addresses strategic possibilities in limiting the successful establishment of introductions.

Reducing the Susceptibility of the Reserve to Invasions

It is generally recognized that different areas of the earth show different susceptibilities to invasions. For example, the World Conservation Strategy cites islands and freshwater systems as particularly vulnerable (IUCN, 1981). Environments characterized by extreme abiotic conditions, such as deserts and arctic ecosystems, are apparently less prone to invasions than moderate environments (Macdonald et al., 1989). Given the fixed set of environmental conditions prevailing within a particular nature reserve, what steps can the manager take to minimize its susceptibility to invasions?

A first step is to maintain the evolutionary perturbation regimes to which the reserve's native biota is adapted. For example, where fire has been infrequent, a change to frequent fires will often disadvantage native species competing with alien species adapted to frequent fires. The invasion of Hawaiian shrublands (Smith, 1985), Mediterranean-type nature reserves throughout the world (Macdonald et al., 1988), and areas in the Neotropics (Parsons, 1972; Janzen, 1986) by grasses are examples of the enhanced susceptibility to invasion of ecosystems where fire regimes have been altered by humans.

Feeding and trampling by large herbivores create perturbation regimes, which often open the door to plant invasions. Alterations to the evolutionary regime are implicated in the invasion of the American intermountain West by *Bromus tectorum* (Mack, 1986), the replacement of the native groundlayer in California by European grasses (Macdonald et al., 1988), and the establishment of many alien plants in Hawaii (Smith, 1985). Where the evolutionary grazing regime is maintained there are indications from Africa that natural grazing can prevent or inhibit establishment of introduced plant species (Macdonald, 1984a, 1985a; Macdonald & Frame, 1988; Macdonald et al., 1987).

In attempting to identify the important perturbation regimes it is necessary to list the "gap-forming" processes in the native communities of the reserves (e.g., Wace, 1986). Each process should then be analyzed to establish if it is likely that the frequency, scale, or intensity of its action has been affected by humans. For example, the frequency of gap formation in the tree layer of many Mediterranean-type woodlands has been increased through lumbering, and this is thought to have accelerated their invasion by alien grasses and forbs (Macdonald et al., 1988). The frequency of peat avalanching on Gough Island in the South Atlantic is greatly increased by human trampling on steep slopes, and the resultant peatslips are rapidly colonized by alien plants (Wace, 1986).

Many introduced plants and animals establish readily in areas subjected to high levels of human disturbance, the so-called "ruderal" weeds and "commensal" animal species. For example, in the Cape of Good Hope Nature Reserve, of the 29 introduced annual plant species present, ten are confined to sites of intense human disturbance, and most of the others occur commonly in such sites (Macdonald et al., 1987). Similarly in the Jasper Ridge Preserve, 38 of a total of 108 introduced vascular plants were restricted to human-disturbed sites (Macdonald et al., 1988). Many introduced plant species proliferate in such disturbed sites and only subsequently invade the adjacent native communities. The strategic considerations that arise from this observation are: (1) to minimize the area of intensive disturbance within a reserve; (2) to locate such sites to minimize the area affected by propagules emanating from them; and (3) to locate the sites in edaphically and climatically atypical or unimportant areas within the reserve. This last consideration is based on the premise that plant species adapted to such areas may be poorly adapted to the typical or important habitats within the reserve. An example is the proliferation of introduced plant species in the highly disturbed lowlands of Hawaii and the general inability of most of these species to invade the high-altitude communities there (Smith, 1985).

The susceptibility of animal communities to invasion by introduced species is poorly understood. There are, however, indications that for vertebrates the predation pressure exerted by a diverse native fauna is important in impeding establishment of introduced species (Macdonald et al., 1986b; Macdonald & Frame, 1988). Reserve managers should accordingly strive to maintain complete communities of predators within their reserves when feasible and compatible with the reserve's other management objectives.

However well a reserve is managed, at least a few alien species will become established. The following sections indicate strategic approaches to the management of established alien species.

Detecting Invasions

Analysis of the histories of alien plant control in a wide range of nature reserves in different biomes and continents has invariably highlighted the importance of early detection of invasions. An example is the ease with which species of *Tamarix* are being controlled in the Organ Pipe Cactus National Monument in Arizona, where the scattered pioneer invaders are hand weeded, as compared with the intractable problem these species pose in the nearby Death Valley National Monument, where they became established in the 1940s (Loope et al., 1988).

Strategic considerations for early detection are:

1. Monitoring the arrival of new species or new infestations of established species should be an important component of the alien plant control program. A good example of this is the *Mimosa pigra* campaign in Kakadu National Park, Northern Territory, Australia (Maddison & Salau, 1986).
2. The frequency of this monitoring should ensure that the new plant/patch doesn't become so well established that it begins spreading to new areas or is prohibitively expensive to remove. The length of the cycle, i.e., the appropriate monitoring frequency, is ecosystem-dependent, for instance, approximately once every five years in a Mountain Fynbos ecosystem, where the main invasive plants require approximately three to six years to reach reproductive age (Stirton, 1978).
3. Reserve staff should receive training in the identification of likely candidate invader species. These should be selected as: (1) species invading similar ecosystems in nearby areas; (2) species invading similar ecosystems elsewhere on the same continent; and (3) species invading similar ecosystems elsewhere in the world. Regional lists of invasive species and field guides to such would be useful (Stirton, 1978).
4. Monitoring should be concentrated on likely invasion sites, e.g., intensive-use areas, boundaries, riverbanks, and walking trails. The whole area of the reserve should be covered at least once during a monitoring cycle.
5. Monitoring should be flexible enough to incorporate the incidental sightings made by reserve staff in the course of their activities (e.g., Macdonald, 1983b).
6. Informed volunteers can help with monitoring (Macdonald et al., 1985).
7. Results from monitoring must become available rapidly enough to permit preemptive action before the infestation "escapes" control.

The ultimate goal for every reserve's alien plant management program should be detection and immediate removal of each new invasion. This situation has recently been reached on Gough Island in respect to new alien plant species (Wace, 1986).

Early detection of new animal invasions is equally important in determining the ease with which the invasion can be controlled. However, monitoring for early detection of introduced animals can often be prohibitively expensive and time-consuming. Fortunately, most vertebrate invasions are relatively easily controlled compared with serious plant invasions (Brockie et al., 1988). Where the invasion is relatively difficult to control (as, for example, feral cats (*Felis catus*) on Marion Island; Van Rensburg, 1986), it is uncertain whether early detection would have markedly improved the ease of control. The "early detection" of a rat (*Rattus* sp.) on Gough Island triggered an enormous

preemptive control effort, which was possibly unwarranted as the species had apparently failed to establish a population on the island (Wace, 1986).

Establishing Control Priorities

Most of the world's nature reserves currently have more invasion problems than there are resources available to combat them. Under these circumstances reserve managers must set their priorities correctly.

However, there are still considerable uncertainties in the prediction of the relative invasive potential of any two species (Brown, 1989), and it is almost impossible to predict the relative impacts of species on the ecosystems invaded (Fryer, 1984). In the face of these uncertainties, setting priorities involves a high element of "ecological guesswork," but this must be attempted rather than failing to set priorities (see Frankel & Soulé, 1981, for an exposition on the need to make decisions in the face of biological uncertainties).

Setting priorities has two major components: targeting introduced species for control and targeting areas within the reserve for control operations.

In choosing which species should be controlled first, intrinsic and extrinsic factors must be considered.

There are four principal aspects of the intrinsic factors (Macdonald, 1984b): (1) the ability of the species to penetrate untransformed ecosystems; (2) its ability to persist there; (3) the ecological impact of its invasion; and (4) the ease with which it can be controlled.

Each one of these aspects can be subdivided into numerous components (Macdonald, 1984b). Even if it is impossible to quantify accurately differences between two species in any of these components, it is normally possible to make a "best estimate" of their relative values. The relative weightings of any of the components or of the four principal aspects noted above provides an important challenge for empirical research. The weightings can only be derived by a retrospective analysis of the realized impacts and subsequent costs of control of a range of well-studied invasions.

The extrinsic factors involved in deciding species priorities relate to such considerations as: (1) the current size of the infestation and the feasibility of total eradication; (2) the likelihood of reinvasion after eradication; (3) the conservation significance of the habitat(s) or species affected by the invasion; and (4) the possibility that the species is a "keystone" alien species, the presence of which facilitates the invasion of the reserve by other alien species (Macdonald et al., 1989).

A species such as fountain grass (*Pennisetum setaceum*), which has a high potential to affect native Hawaiian ecosystems adversely (Smith, 1985), might be the top-priority species for control in a Hawaiian national park but still relatively localized in occurrence within the reserve. However, if it becomes apparent that eradication or maintenance of it at densities compatible with the reserve's conservation objectives is impossible, and that reinvasion from areas adjacent to the park is inevitable, it might be assigned a lower priority for control (Brockie et al., 1988).

Once it has been accepted that an introduced species cannot be eradicated from a reserve or maintained below an acceptable density threshold, given current control technology and control resources, three strategic approaches are possible and, generally, all three should be employed: (1) An attempt should be made to increase the allocation of resources to the control effort. (2) Efforts should be made to improve control technology through appropriate research. In many cases biological control methods are applied at this stage. Examples are *Salvinia molesta* in Kakadu National Park (Macdonald & Frame, 1988), *Passiflora mollissima* in Hawaiian national parks (Gardner, 1986), and the cat on Marion Island (Van Rensburg, 1986). (3) A policy can be adopted of controlling the species within only a portion of the reserve. In many cases this strategy can be viewed as a holding action until control technology is improved.

In developing a strategy based on intensive alien control areas within a reserve the following considerations should help define the extent and location of these areas: (1) the feasibility of keeping

the alien species under control in these areas, given current technology and current levels of funding; (2) the extent to which the communities included within the control areas represent the reserve's total biota; (3) the inclusion of any high-priority conservation areas/species within the control areas; (4) the inclusion of any key areas for the maintenance of important ecological processes within the reserve. An example of this would be the exclusion of feral water buffaloes (*Bubalus bubalis*) from the groundwater recharge zones of the monsoon forest patches in Kakadu National Park (Macdonald & Frame, 1988); (5) the spatial distribution of the control areas with respect to their possible future roles as sources of propagules for recolonization of the remainder of the reserve by native species once control is achieved there. Where the dispersal biology of important native species is known, McClanahan (1986) provided a theoretical framework for such an approach.

A good example of the application of the "intensive control area" strategy to alien plant control in a nature reserve has recently been presented for the Hawaii Volcanoes National Park (Tunison, 1986). The localized control of mongooses (*Herpestes auropunctatus*) in the breeding areas of endangered bird species in the Hawaiian national parks is an example of the application of the strategy to a problem with introduced animals (Keith et al., 1986; Brockie et al., 1988). This approach should be viewed as a temporary holding measure: to accept it as a final solution is to surrender the excluded portions of the reserve. This is particularly the case where the alien species is capable of transforming the ecosystems it invades, as certain alien grasses in the Hawaiian national parks can do (Smith, 1985). Before resorting to this strategy, every other possibility should be exhausted. This includes analysis of current control operations to ensure that they are being applied effectively.

Planning and Executing Control Operations

Unless it is obvious that the extent of the invasion is so small that its control poses no problem, the following systematic approach should be adopted:

1. Ensure that the most economical method of removing/killing the invading species is in use. Often the optimum method varies with the age of the individual to be treated, the density of the infestation, and the terrain. Where multi-species invasions are to be treated simultaneously, the decision as to which techniques should be used can become extremely complex. Under these circumstances computerized optimization techniques should be employed when possible.

2. Quantify the extent of the invasion. The range, density distribution, age-class distribution, and reproductive characteristics of the invading species within the reserve or intensive control area should all be known.

3. Use the information from (1) and (2) to plan the removal operation within budgetary constraints. At this stage it is essential to define objectively the acceptable density of the alien species within the reserve if total eradication (which is always the preferred option) is considered impossible. If these calculations show that the required control objectives can be achieved within the desired time period, the control operation should be initiated. If not, either these objectives will have to be modified or strategies must be adopted to improve the control effort or its efficiency (see previous section).

4. Where the control operation is complicated by reappearance of the invading species in areas cleared of it, follow-up must be planned. A good example of this is the problem posed by the regeneration of Australian *Acacia* species from soil-stored seed in the Cape of Good Hope Nature Reserve (Macdonald et al., 1988).

5. Where reinvasion of cleared areas from elsewhere occurs, the control strategy must aim to minimize the extent of this reinvasion. Reinvasion by the alien house sparrow (*Passer domesticus*) has led to the failure and abandonment of control operations in most southern African reserves

(Macdonald, 1988a; Macdonald & Frame, 1988), with the only successful campaign being known from the extremely isolated Ugab outstation in the Skeleton Coast Park in South West Africa/ Namibia (Macdonald & Nott, 1987). It was only when fences were employed to limit reinvasion by goats (*Capra hircus*) in the Hawaiian national parks that control operations became successful (Macdonald et al., 1989).

Wherever there are directional drifts of propagules into the area to be cleared, e.g., from a boundary or from a river, the planning of the control operation must take these into account. In general, it is desirable to initiate control at the source of such a propagule drift; not doing so can cause the control effort to fail. An example of such failure is the clearance of the invading shrubs *Datura innoxia* and *Nicotiana glauca* from small portions of riverbeds in the Skeleton Coast Park. Reinvasion from upstream following the next flood produced equally dense reinfestations (Loope et al., 1988). Control in these situations will only be effective if the upstream catchment areas are cleared first (Macdonald, 1988b). A system of buffer zones can be considered for limiting reinvasion of cleared areas.

6. In many cases an important strategic decision has to be made as to whether dense infestations should be treated before or after the outlying low density infestations. This complex choice depends on such factors as the relative costs of clearing stands of different density, the contribution of stands of different size to seed input into surrounding areas (McClanahan, 1986), and the rate of reestablishment of native species following removal of stands of different density and age. Normally the optimum strategy is first to clear the outlying sparse infestations, as this secures the greatest area of relatively intact native communities at the least cost (e.g., *Acacia cyclops* in the Cape of Good Hope Nature Reserve; Taylor et al., 1985). For *Pinus pinaster* infestations in Mountain Fynbos, where dense stands older than approximately 15 years show an evident reduced ability to regenerate native plant communities following clearance (Macdonald & Richardson, 1986), reversal of this strategy might be best.

7. In all control campaigns, deleterious side effects of the control methods must be avoided or minimized (see Macdonald et al., 1989, for discussion of the trade-off between short-term deleterious effects and long-term benefits of control). In particular, care should be exercised to ensure that these methods do not slow reestablishment of the native community.

8. Rapid reestablishment of the native plant community often serves to reduce markedly the extent of reinvasion or regeneration of the alien species being controlled (e.g., Wace, 1986). In some cases it can prevent a whole range of secondary invasions that otherwise could follow the removal of the primary invasion (e.g., the secondary invasion of Mountain Fynbos areas cleared of *Hakea sericea* by *Acacia longifolia,* which is more difficult to control; Pieterse & Cairns, 1986). In some instances planting native species in cleared areas has been undertaken to speed up the regeneration of the native community. For example, the fast-growing native forest pioneer *Trema orientalis* has been planted in sites cleared of *Chromolaena* (*Eupatorium*) *odorata* in the Vernon Crookes Nature Reserve in Natal. However, in comparative trials it turned out that planting *T. orientalis* following the clearance of *C. odorata* in Durban's municipal nature reserves gave little improvement in the rate of revegetation in comparison with unaided natural regeneration (Nichols, 1985). Such expensive practices obviously warrant careful testing.

9. In all cases the control operation must be carefully planned, and the plan stating quantitative objectives and deadlines should be committed to paper, preferably as part of the reserve's overall management scheme. The allowance each year for increased follow-up as a result of the previous year's additional primary clearance is critical. All control operations must be fully documented and mapped to allow for follow-ups regardless of changes in staff. The control operations and the achievement of the program's stated objectives must be monitored continually (e.g., Macdonald, 1983c). Where these objectives are not achieved, the program must be reevaluated and alternative strategies or new techniques adopted. It might even be necessary to redefine objectives in light of experience gained. Whatever happens the operation should not simply be dumped on the ever-growing pile of failed control programs. Even a failure, if carefully analyzed, can lead to improved management.

Conclusion

Although the current situation with regard to introduced species in the world's nature reserves does not allow complacency (Macdonald et al., 1989), there are grounds for cautious optimism. This is possible, not only because of an increased awareness of the problems posed by invasions, but also because of recent improvements in control technologies, e.g., carefully practiced biocontrol techniques (Gardner, 1986; Moran et al., 1986; Pemberton, 1986).

If reserve managers take advantage of recent advances in our understanding of biological invasions, they can incorporate a predictive element in their management approaches. For example, they can know roughly which species, or type of species, can be expected to invade their reserves, and which areas within their reserves are most likely to be invaded. In addition, our understanding of the invasion process itself now allows management to be aimed at minimizing the competitive advantage of introduced species.

The systematic approach to the problem that is inherent in the above strategies can be presented more simply as a series of steps (e.g., Macdonald, 1985b), which could be readily transformed into an "expert-systems" computer program. This systematic approach should serve to improve the prognosis for future control operations. As a generalization, past control programs have been poorly conceived and poorly executed. As a result, the history of the control of introduced species in nature reserves has led to an unduly pessimistic prediction of our future success rate in this important field of conservation management.

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PLANTAS INTRODUCIDAS EN LAS ISLAS GALAPAGOS[1]

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Resumen

Se analiza el creciente número de plantas que son introducidas a las islas Galápagos, quedando demostrado que actualmente se conocen unas 260 especies ajenas, de las cuales algunas son muy agresivas, de tal forma que están invadiendo áreas silvestres, constituyendose en uno de los mas graves problemas para el manejo del Parque Nacional Galápagos. Las plantas introducidas mas agresivas y su posible manejo es discutido en este trabajo, ya que constituyen una grave amenaza, no solamente para las áreas del Parque Nacional, sino también para los pastos y cultivos de las áreas agrícolas.

El número conocido de especies de plantas ajenas en Galápagos ha crecido rapidamente durante los últimos años posiblemente debido al aumento de la población humana, sus necesidades y deseos por plantas ornamentales, de cultivos, medicinales, maderables, etc. Con el gran flujo de gente y carga del continente americano hacia Galápagos, las introducciones accidentales deben tener un papel mas importante que antes, a mas de las introducciones intencionales.

Las especies introducidas de plantas, su distribución e impacto en la vegetación nativa han sido tratadas en varios trabajos (e.g., Wiggins y Porter, 1971; Eckhardt, 1972; Eliasson, 1972; Schofield, 1973; Black, 1974; Hamann, 1974; van der Werff, 1977, 1979; Hamann, 1979a, b; de Vries y Tupiza, 1980; Hamann, 1981, 1984; Loung y Toro, 1985; Cruz et al., 1986; Lawesson, 1986; Lawesson et al., 1987; Loung, 1987; Loung y Potts, 1987; Utreras, 1987; Macdonald et al., 1988). Con estos trabajos está conocido que el numero de plantas introducidas ha crecido de 77 especies reportadas en 1971 (Wiggins y Porter, 1971) a casi 260 especies (Lawesson et al., 1987). Es decir que mas de 10 especies extranjeras han sido introducidas a Galápagos cada año desde 1970.

Aunque la mayoría de las especies no han cambiado el equilibrio ecológico significativamente, especies como *Psidium guajava, Lantana camara, Eugenia jambos, Cinchona succirubra, Pennisetum purpureum, Rubus* sp., y otras han invadido áreas silvestres, formando vegetación monoespecífica, tal vez tipos de vegetación muy diferentes a los originales. La flora introducida por esta razón causa mucha preocupación.

Este trabajo contiene una apreciación de las especies mas agresivas, y se discute la historia de la invasión con su impacto en la vegetación nativa y los problemas de manejo que causan.

Categorias de Plantas Ajenas

La flora de las Islas Galápagos puede ser dividida en dos grupos de acuerdo a su origen: 1) Plantas indígenas (596 taxa, Lawesson et al., 1987) y 2) Plantas ajenas (no-indígenas) que en una u otra

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manera fueron traidas a Galápagos por el hombre (254 taxa, Lawesson, este symposium). Hay dos tipos de plantas introducidas: las que fueron traidas accidentalmente, tipo "I" (Introducidas), sin ningún intento de hacerlo, como en suelo, carga, embarcaciones, ropas, etc. Ejemplos: *Synedrella nodiflora, Sonchus oleraceus, Porophyllum ruderale, Plantago major;* y las introducidas intencionalmente, tipo "C" (Cultivadas).

Estas plantas ya existen en Galápagos para su uso forestal (*Triplaris cumingiana, Pinus radiata, Cedrela odorata, Casuarina equisetifolia, Tectona grandis, Cordia alliodora*) uso agrícola (*Pennisetum purpureum, Saccharum officinarum, Beta vulgaris, Coriandrum sativum, Phyllanthus acidus*), uso ornamental (*Nerium oleander, Impatiens balsamina, Dahlia variabilis, Tagetes erecta, Hibiscus rosa-sinensis, Lantana camara*), uso medicinal (*Cinchona succirubra, Ricinus communis, Datura arborea, D. stramonium*), y uso fructicultural (*Psidium guajava, Terminalia catappa, Annona muricata, Carica papaya, Manihot esculenta, Rubus* sp., *Eriobotrya japonica*).

En Lawesson (este symposium) están dadas las especies introducidas.

Distribucion y Dispersion en Galapagos

Las plantas del grupo C generalmente están restringidas a las islas pobladas que son Santa Cruz, San Cristóbal, Florena, Isabela Sur, y Baltra, aunque algunas plantas remanentes de la colonización humana todavía pueden ser encontradas en Isla Santiago, como *Datura stramonium, Persea americana,* y *Citrus* sp. Las plantas accidentalmente introducidas (I) están mucho mas ampliamente distribuidas, debido que se dispersan en algunos casos con el hombre, en su ropa, zapatos, etc. Para detalles sobre la distribución ver Lawesson et al. (1987), y Macdonald et al. (1988).

Aunque la mayoria de especies ajenas estan restringidas a las areas pobladas, existen algunas plantas introducidas en virtualmente cada isla, también en Fernandina, parte Norte de Isabela, y otras islas. Grandes numeros de turistas visitan áreas normalmente muy aisladas como Fernandina y Espeñola, y no es extraño que las primeras observaciones de plantas ajenas frecuentemente sucedan junto a los senderos turisticos como Punta Suarez en Española, donde se encontró *Cucumis dipsaceus* la primera vez en 1983 (Loung y Toro, 1985) o como el caso de *Cleome viscosa,* que fue encontrada por primera vez en Baltra hace 30 años, pero que ahora existe en Santa Cruz, Daphne, Santiago, Tagus Cove (Isla Isabela), todos sitios usados por turistas. También se dispersan facilmente algunas plantas ajenas junto a las carreteras (Schofield, 1973).

Las Plantas Agresivas

Aunque existen plantas ajenas en todo el archipiélago, el impacto que causan es muy variable. Algunas especies, principalmente del tipo "I" se encuentran en comunidades vírgenes pero sin alterar el sistema (como *Sonchus oleraceus* en Volcán Wolf y Volcán Darwin). Mas grave es la situación con algunas de las plantas leñosas del tipo (C), que en las islas pobladas están cambiando el ecosistema considerablemente, como es el caso con *Psidium guajava* en las cuatro islas más grandes. Las plantas agresivas están caracterizadas por su buena dispersión, capacidad de invadir, y reemplazar vegetación nativa. A continuación se discutirán algunos ejemplos de las especies mas agresivas. *Cinchona succirubra,* una de las especies mas agresivas en Galápagos, han sido discutido por Macdonald et al. (1988).

Psidium guajava L. (Myrtaceae). Esta especie originaria de América tropical es la planta ajena que cubre las mas extensas áreas en Galápagos. Fué introducida en 1869 a Galápagos para sus frutas. En Isla Santa Cruz no fue reportada en la literatura antes de la publicacion de la *Flora of the Galápagos Islands* (Wiggins y Porter, 1971), y varios investigadores atestiguan que su distribución en esta isla era muy restringida 20 años atras, limitada a pequeñas plantaciones en el area agricola (S. Itow, pers. com.).

En los últimos 40 años la guayaba se ha dispersado de las áreas agrícolas hasta grandes extensiones en las cuatro islas grandes. En Isla Isabela, donde se ha cultivado *Psidium guajava* mayor tiempo, la especie probablemente se dispersó a muy grandes áreas en todo el lado sur de Volcán Sierra Negra temprano en este siglo. Ahora la distancia de Santo Tomas hasta Alemania (40 km) está ocupada en gran parte por bosques de guayaba. También el lado este del Volcán Sierra Negra esta ocupado por bosques y vegetación de arbustos principalmente de esta planta, con una buena sobrevivencia y virtualmente imposible de eliminar (de Vries y Tupiza, 1980). En Santa Cruz ahora existe guayaba en toda la parte alta desde el área agrícola hasta las partes centrales de la isla cerca los de cerros Crocker, Puntudo, y Los Gemelos. En San Cristóbal toda el área alta de la isla está ocupada en mas o menos alto grado, inclusive cerro San Joaquin, Laguna El Junco, y las cuencas en la parte Sureste. Además, existen poblaciones de *Psidium guajava* en el Volcán Cerro Azul; no es conocida su manera de llegada, pero este volcán ha sido visitado frecuentemente por colonos, y esto puede explicar la presencia de la especie.

Psidium guajava se dispersa facilmente por semillas, que son comidas por varias especies de pinzones y otros pájaros, igual por animales domésticos como vacas y chanchos, que durante años han funcionado como vectores de las semillas. Hasta pocos años atrás estos animales domésticos pastaban libremente en áreas silvestres del Parque Nacional Galápagos (PNG), y de esta manera las semillas de guayaba fueron dispersadas (van der Werff, 1979). En ciertas áreas como Sierra Negra, Volcán Cerro Azul, y Floreana todavía sucede esto. Estos antecedentes históricos y biológicos pueden explicar la amplia distribución que *Psidium guajava* tiene ahora en las cuatro islas pobladas, representando serios problemas para el manejo de las áreas del PNG, además para el buen uso de las áreas agrícolas. Ahora se estima que se extiende 20,000 ha en Isabela, 12.000 ha en San Cristóbal, 8,000 ha en Floreana, y 100 ha en Santa Cruz, total mas de 40,000 ha. El impacto en la vegetación nativa ha sido comentado en varios trabajos (van der Werff, 1979; Hamann, 1984). La combinación de destrucción de la vegetación por animales domésticos y la dispersión siguente por los mismos ha tenido un serio impacto en todas las islas pobladas, reemplazando o eliminando vegetaciones nativas como bosque de *Scalesia pedunculata*, arbustos de *Miconia robinsoniana*, y vegetación de *Sphagnum* y de *Cyathea weatherbyana*.

Psidium guajava y otras especies relecionadas (e.g., *P. cattleianum* Sabine) causan problemas en otras partes similares a las que existen en Galápagos.

Los ejemplos mejor documentados probablemente son de Africa Sur (Macdonald, 1983) y Hawaii (Gardner y Davis, 1982). Existe muy poca literatura sobre el control de especies de *Psidium*, haciendo su control en Galápagos difícil. Los esfuerzos de control han sido restringidos a Santa Cruz, debido a razones económicas y logísticas. También el área relativemente pequeña en esta isla argumenta para empezar aqui una experimentación. El uso de métodos manuales fué iniciado por el Servicio Parque Nacional Galápagos (SPNG) en 1971, y en 1974 se inició el uso de herbicidas. No hay precisión de cuales herbicidas se usaban, y los resultados de los ensayos no fueron publicados. Una nueva serie de experimentos con herbicidas fué efectuada durante 1982 (Utreras, 1987) en áreas agrícolas y de PNG, usando cuadrantes permanentes con un área total de 4,400 m^2, y los herbicidas Tordon 101, D.M.A 6, y Ceretox Ester 334. Varios métodos de aplicación fueron usados, y los resultados preliminares indicaron que los tres herbicidas funcionaban igual matando a los árboles de guayaba. Nunca fué posible repetir las aplicaciones con los mismos buenos resultados. Además nuestras nuevas revisiones de los árboles tratados que no murieron, indican que pudieron rebrotar después de algun tiempo. El SPNG inicio otra serie de ensayos en 1984 con herbicida Tordon 101 en dosis de 5, 25, y 30 cm^3 mezclado con Kerex, aplicado a 5 y 30 cm de altura del tocón, en el área agrícola cerca de Bellavista en el camino a M. Luna (C. Arturo Informe de Actividades, 1984). Pero un informe técnico no existe. Aparentamente ni en Galápagos ni en otras partes se ha logrado hasta ahora encontrar una efectiva manera de controlar *Psidium guajava*. A nivel local en Galápagos con buldozer se ha eliminado guayaba, sembrando pastizales inmediatamente después.

Asi se cubre el área rápido con un pasto (e.g., *Pennisetum purpureum*, pasto de elefante) que no

permite muchos rebrotes de guayaba. Este método solamente es factible en pequeñas áreas de cultivación. Las áreas de PNG todavía se encuentran con serios problemas en conexión con *Psidium guajava*, y una solución de su manejo y menos su erradicación no parece realista en poco tiempo.

Lantana camara (Verbenaceae). Esta especie se usa para ornamento en áreas subtropicales y tropicales. Con su buena capacidad de dispersión y reproducción vegetativa, y por semillas, ha crecido a una de las mayores plantas ajenas problemáticas en algunas áreas como Australia (Bartholomew, 1980), Africa Sur (Macdonald, 1983), y Hawaii (Gardner y Davis, 1982). También en Galápagos *L. camara* representa un serio problema en la conservación y manejo de las áreas silvestres del PNG y en áreas agrícolas. Se dispersa facilmente por sus semillas, que son comidas por los pinzones.

Lantana camara fué introducida a Floreana en 1938 (Cruz et al., 1986). Hasta 1972 aparentemente no causó mayores problemas. Eckhardt (1972) informó "*Lantana* ha sido también encontrada en Galápagos, en Floreana, pero hasta ahora no parece dispersarse mucho, tampoco ha causado mucho daño." Por el contrario en 1987, un área aproximada de 2,000 ha en la parte alta (entre 200 y 400 m) esta ocupada en Floreana, especialmente cerca de Cerro Pajas. Los lados exteriores, antes cubiertos por vegetación de *Scalesia pedunculata*, ya se encuentran con una vegetación monoespecífica de *L. camara*, solamente con pocos remanentes de *Scalesia*.

También cerca de Cerro Wittmer y en el área agrícola se encuentran poblaciones de *Lantana*. La presencia conjunta de *Lantana camara* y *Psidium guajava* causa gran preocupación, ya que las dos especies ajenas están exterminando varios tipos de vegetación y especies de plantas y animales endémicos (Cruz et al., 1986). Los mas graves problemas con *Lantana* existen en Isla Floreana, pero también recién ha sido introducida a Santa Cruz y San Cristóbal. Hace 10 años Alf Kastdalen, un residente de Santa Cruz, hizo una compaña de eliminación de *Lantana camara* en esta isla, con buen éxito y fué erradicada (de Vries, pers. com.). Recién se ha introducido de nuevo, y en Agosto de 1987 se observó *Lantana* en cultivo en los pueblos de la isla, y también en varios sectores del área agrícola. También fué encontrada en el camino turístico de Puerto Ayora hasta Bahia Tortuga (los autores, pers. obs.).

Entonces *Lantana camara* está en proceso de dispersarse a una mayor área en Santa Cruz, y se puede esperar una situación similar en esta isla como la que se presenta en Floreana. En San Cristóbal existe ahora muchas plantas de *Lantana camara*, inicialmente cultivado en la mayor población Baquerizo Moreno, donde se observó la primera planta en 1985 (los autores, pers. obs.). En 1987 se encontró *Lantana* hacia la parte alta de la isla, ocurriendo en los filos de la carretera que une P. Baquerizo Moreno y El Progreso. También fué encontrada en algunas de la cuencas en la parte sureste, alrededores del pueblo Los Arroyos, carretero que une el Junco.

Aunque en menor escala también está ocurriendo un proceso de dispersión rapida en esta isla. *Lantana camara* no ha sido reportada en Isabela. La existencia de una especie ajena de *Lantana* en Galápagos es seria, a pesar que existe una especie nativa *L. peduncularis*. Es posible que ésta especie pueda formar híbridos con *L. camara* y de esta forma hacer imposible la erradicación o control de la especie ajena.

Intentos locales de eliminar *Lantana camara* de áreas agrícolas han sido exitosos en Floreana, donde finqueros han usado el método de arrancar las plantas con sus raices, y después fumigar los rebrotes y nuevas plantas con herbicidas como Tordon (F. Cruz, pers. com.). En 1987 algunas áreas agrícolas fueron limpiadas con buldozer provisto por el Instituto Nacional de Galápagos (INGALA) en este tiempo construyendo una carretera en Floreana. Aunque han sido planificadas actividades de control de *Lantana* en la isla en dos años por SPNG y ECCD, 1986, 1987, la falta de financiamiento ha hecho la iniciación imposible. En las islas de Santa Cruz y San Cristóbal la erradicación de *Lantana* todavía es posible sin la inversión de muchos recursos económicos, como lo demostrado por Kastdalen 10 años atrás. En Junio 1987 la ECCD y SPNG lanzaron un folleto sobre *Lantana* y su impacto nocivo en el ambiente y áreas agrícolas (Anónimo, 1987), esperando que una campaña de educación combinada con erradicación local en fincas, poblaciones, y carreteras pueda solucionar este problema en Santa Cruz y San Cristóbal.

En Floreana una inversión a otro nivel de financiamiento, personal, y material es necesario para al menos controlar la dispersión de esta especie. Un esfuerzo conjunto entre la población y los autoridades de manejo debe ser establecido para cumplir con una cuestión tan difícil.

Kalanchoë pinnata (Lam.) Pers. (Crassulaceae). Este ornamento es probablemente de origen africano. Con su carácter suculento es capaz de sobrevivir y reproducirse en climas secos, igual como en áreas húmedas. Tiene una alta capacidad de reproducirse vegetativamente por las hojas. Por esta razón se encuentra ésta planta especialmente en la vegetación de las áreas costeras en Galápagos (dry zone, fide Wiggins y Porter, 1971) pero también en las zonas de transición y húmedas. Es una de las pocas especies ajenas en Galápagos que puede sobrevevir y dispersarse en zonas secas. De otras especies con este poder se puede mencionar *Fucraea cubensis*, *Cucumis discaceus*, y *Delonix regia*. La historia de la invasión no es bien conocida, pero es claro que *Kalanchoë* existió en Wreck Bay, San Cristóbal en 1905–1906, de donde fué reportada por Stewart (1911) como *Crassuvia floripendia* Comm., "cerca habitaciones." Es probable que fué introducida a San Cristóbal o Floreana primero. Aparentemente no tomó mucha atención o dominancia la planta en la vegetación hasta pocos años atrás, a pesar que ningun autor menciona la planta después de Stewart hasta antes de la publicación de la *Flora of the Galápagos Islands* (Wiggins y Porter, 1971).

Esto es probablemente debido a su lenta dispersión. Los propágulos de las hojas no se dispersan mucho, pero la alta cantidad producida puede alcanzar a invadir vegetación cerrada a largo plazo.

En 1987 *Kalanchoë pinnata* está en el área del puerto en San Cristóbal hasta Progreso, entre nivel del mar y 250 m, en altas concentraciones junto con *Furcraea*, afectando un área posiblemente de hasta 500 ha. También se encuentra junto al cerro San Joaquin a 600 m. En Isabela la planta abunda en toda el área agrícola de Santo Tomás, que se ubica entre 300 y 400 m. En Santa Cruz *Kalanchoë* es encontrada en los límites del área urbána en el camino antiguo a Bellavista, en la zona agrícola a 100 m hasta Santa Rosa, 400 m. Está estimado que 50 hectáreas están afectadas por *Kalanchoë* en cada isla Isabela y Santa Cruz.

En Floreana *Kalanchoë* tiene alta dominancia en el camino desde un poco arriba de Black Beach hasta el área central agrícola, donde varios tipos de vegetación de transición y bosque siempreverde están invadido y especialmente hierbas nativas están siendo reemplezadas por *Kalanchoë*. Una estimación tentativa del área afectada puede estar entre 50 y 100 hectáreas.

Debido que esta planta aparentemente recién está creciendo en su impacto e importancia, hasta ahora no se ha iniciado ningun intento de control o manejo. Sin embargo, aunque tiene una dispersión lenta, representa una planta que puede a largo plazo producir cambios en los ecosistemas.

Passiflora edulis Sims y otros. (Passifloraceae). Las trepadoras de la familia Passifloraceae son conocidas como plantas con buena capacidad de invadir vegetación nativa, cuando son introducidas en áreas fuera de su distribución natural. *Passiflora* es un género de América, con pocas especies fuera de América del Sur. *Passiflora mollisima* causa problemas en Hawaii (Warshauer et al., 1983), y *P. foetida* en Australia (Skeat, 1986). En Galápagos han sido introducidas tres especies: *Passiflora edulis* Sims, *P. ligularis* Juss. (Fig. 1), y *P. quadrangularis*, que son cultivadas en la parte continental del Ecuador (Holm-Nielsen et al., 1988). Las frutas son usadas en varios tipos de jugos o consumidas frescas. Las semillas pueden ser dispersadas por pájaros, ratas, y otros. No está documentado cuando fueron introducidas, pero no fueron mencionada por Wiggins y Porter (1971) ni por Eckhardt (1972). Probablemente existieron en este tiempo en algunas fincas, pero no en áreas silvestres como es observado ahora. En Santa Cruz se han distribuido *Passiflora edulis* y *P. ligularis* hacia áreas de PNG, en zonas secas y húmedas, respectivamente. *Passiflora edulis* ya existe en varios sitios de Puerto Ayora hasta Bellavista, en el área de ECCD y SPNG, y también en el lado norte de la isla, desde Los Gemelos hasta el canal de Itabaca. También en varios sitios del área agrícola en Santa Cruz se ven árboles y arbustos cubiertos por la especie. Entonces tiene una distribución entre 0–400 m. *Passiflora ligularis* está restringida a ambientes mas húmedos, donde esta trepadora puede crecer rápido y dominar la vegetación.

FIGURA 1. *Passiflora ligularis*, una neuva especie, recién introducida a Galápagos.

El área infestada por *P. ligularis* está cerca del Cerro Crocker, Los Gemelos, y el pueblo de Santa Rosa, entre 400 y 600 m. En las otras islas también existen las *Passiflora*, aunque la distribución detallada no es muy clara todavia; pero parece que una disperción desde los cultivos a mas grandes áreas agrícolas y silvestres está en proceso. Esto probablemente pasa por medio de ratas y pájaros, especialmente varias especies de pinzones (los autores, pers. obs.).

Como es el caso con *Kalanchoë*, no se ha prestado atención a las especies ajenas de *Passiflora* y su impacto a las biotas de Galápagos. A pesar de su buena capacidad de dispersión y rápido crecimiento en épocas de clima favorable, por lo que es necessario considerar medidas de control a corto plazo, para no llegar a condiciones como las de Hawaii. Con un esfuerzo masivo, es posible todavía eliminar la mayoría de *Passiflora* en el PNG de Santa Cruz, dado que el área afectada es relativamente pequeña. La manera de erradicación aparentemente es posible, e.g., cortar el tronco principal basalmente, y toda la planta y sus raices van a morir (Macdonald et al., 1987). Las plantas ajenas de *Passiflora* no pueden ser confundidas con plantas nativas, por lo cual se puede activar grupos de voluntarios o las población humana local para hacer campañas locales de erradicación.

Rubus spp. (Rosaceae). Está documentado que en algunas otras islas tropicales y subtropicales las especies de *Rubus* pueden ser invasoras agresivas, causando graves problemas en el manejo de áreas silvestres, como lo observado en Isla Reunión (Macdonald, pers. com.), Madagascar y Isla Mauritius (Hamann, pers. com.), y Hawaii (Gardner y Davis, 1982).

Con estos antecedentes es de mucha preocupación el hecho que hace tres años una o posiblemente dos especies de *Rubus* han sido introducidas a Galápagos, especificamente a San Cristóbal y Santa Cruz, para cultivar las plantas y usar sus frutas para jugos y mermaladas. Igual el hombre como los pájaros comen las frutas, y las semillas entonces se dispersan rápido. Además de la capacidad de extender su área por medio de semillas, también puede crecer la misma planta por estolones algunos metros en poco tiempo con el clima favorable de Galápagos. *Rubus* fué introducida a San Cristóbal en 1983 (colonos, pers. com.) para cultivación. Fué traida de la región de Ambato en la parte

continental del Ecuador. Se empezó a cultivarlo en el área de Cerro Verde, en la parte sureste de la isla. En Octubre 1985 el autor principal visitó San Cristóbal, y solamente se observó plantas de *Rubus* cerca de los pueblos de Cerro Verde y Los Arroyos, y en poca cantidad. En Noviembre de 1986 se visitó las mismas áreas, y se observó la mayoría del área entre Cerro Verde y la costa cubierto por una densa capa de *Rubus*, avanzando 10–15 m de la carretera hacia dentro de la vegetación. También se observó muchas plantas de *Rubus* entre Cerro Verde, Cerro Pelado, cerca de la laguna de El Junco y además las cuencas de La Toma y La Honda.

En Junio de 1987 el problema alcanzó dimensiones alarmantes ya que los márgenes del carretero en el área de Cerro Verde se encuentran cubiertos por *Rubus* que alcanzan hasta 5 m de altura, y el proceso de dispersión respecto a reportes anteriores se amplía a áreas de El Progreso, Junco, encañadas la Toma el Plátano, Cerro Verde, Las Goteras, y El Chino, es decir practicamente toda la zona agrícola está en proceso de ser invadida, habiendo entrado ya en áreas de Parque Nacional.

Rubus entonces en poco tiempo se ha dispersado de algunas plantas hasta influir en un área superior a 3,000 hectáreas proximadamente ubicadas entre 100 y 600 m.

Rubus también se encuentra en Santa Cruz, donde fué introducida hace dos años (colonos Santa Rosa, pers. com.). Existen matorrales de *Rubus* fuera de cultivación en Santa Rosa y el Carmen, que se ubican entre 300 y 400 m. Una dispersión similar a lo que pasa en San Cristóbal entonces es probable.

Dada su introducción a Galápagos hace poco tiempo, medidas de control o manejo no han sido iniciadas todavía. Sin embargo es necesario hacer algo al respecto ahora para limitar la dispersión a todas las áreas de Santa Cruz y San Cristóbal. Igual es importante evitar que sea introducida a otras islas en el archipielago. Medidas de control para *Rubus* no son conocidas, aunque varias iniciativas de experimentación biológica han sido probadas en diferentes partes (Gardner y Davis, 1982). Especialmente en Santa Cruz, todavía parece posible erradicar las plantas de *Rubus*, antes que se disperse a toda la isla. La situación evidentemente es mas difícil en San Cristóbal. En ambas islas, una cooperación entre las diferentes autoridades y la población local es necesaria para alcanzar el éxito.

OTRAS PLANTAS AGRESIVAS

Existen otras plantas ajenas que están invadiendo áreas silvestres en una forma agresiva. Estas en su totalidad fueron introducidas a Galápagos para ser cultivadas (grupo C), y por razones de mal manejo se han escapado a áreas de PNG. Normalmente cubren áreas menores que las mas agresivas mencionadas anteriormente. Una excepción es *Pennisetum purpureum* (Fig. 2) que debido a su amplio uso en áreas agrícolas, tiene una cubertura probablemente de mas que 5,000 hectáreas. También, *Eugenia jambos* (Fig. 3) debe ser mencionada, no tiene muy amplia distribución, pero debido a su manera de crecimiento, formando densos bosques monospecíficos, que no permiten a otras plantas sobrevivir. *Eugenia* tiene un fuerte impacto en la vegetación natural, donde existe y se amplia. Debe ser controlada ahora antes que áreas mas amplias sean cubiertas, especialmente en la Isla San Cristóbal donde existen grandes áreas con esta planta.

El árbol *Cedrela odorata* (Meliaceae) fué introducido 30 años atrás, y aparentemente no presentó problemas para la conservación. Dado el amplio uso de su madera para construcciones y otros, se ha sembrado esta especie en Santa Cruz y San Cristóbal en los cercos y limites especialmente. Hace 5 años los árboles mas grandes empezaron a producir flores y frutas, y las semillas se dispersan facilmente con los vientos. Por lo mismo *Cedrela odorata* ahora está en proceso de dispersarse desde el área agrícola en Santa Cruz hacia las áreas altas de PNG. En 1986 se encontraron las primeras plantas de *C. odorata* en el bosque de *Scalesia pedunculata* en los sitios Los Gemelos y Cerro Crocker (los autores, pers. obs.).

FIGURA 2. *Pennisetum purpureum*, una graminea, que ha invadido grandes areas en las islas pobladas. El foto está tomado en partes altas de Santa Cruz, en la zona de *Miconia*, Julio 1987.

Melia azedarach (Meliaceae) es otra especie introducida a Galápagos para usos ornamentales. La especie es identificada como la segunda mas agresiva planta en partes de Sur Africa (Macdonald, 1983). Solamente existe en cultivación en las cuatro islas pobladas, pero una lenta dispersión fué observada en diciembre de 1986 en la parte alta de Floreana (los autores, pers. obs.). Con los antecedentes de otras partes no es recomendable cultivar esta planta en Galápagos, donde aparentemente existen buenas condiciones para la mayoría de plantas ajenas.

Furcraea cubensis (Agavaceae) es una planta de los valles secos interandinos, y resiste climas secos. Está introducida en las cuatro islas pobladas, donde se establece desde el nivel del mar hasta 800 m (en Santa Cruz). Tiene una dispersión aparentemente lenta, pero produce una alta cantidad de semillas, que al igual que *Kalanchoë* invade vegetación cerrada. Especialmente en San Cristóbal e Isabela existen poblaciones de *Fucraea* en grandes áreas costeras, pero también en áreas altas de Santa Cruz y Floreana es significativa.

CONCLUSIONES

Existe una diversidad de plantas ajenas traidas a Galápagos por el hombre y están causando graves problemas en el archipielago.

Virtualmente ninguna isla está sin plantas ajenas, aunque las islas pobladas, especialmente Santa Cruz, contienen los mas altos números. También en las islas pobladas se ven los mas graves problemas de conservación, debido a la invasión de extensas áreas silvestres y agrícolas por especies ajenas, que compiten efectivamente con la vegetación nativa, en algunos casos cambiando el ecosistema original considerablemente. El número de plantas agresivas probablemente va a seguir

FIGURA 3. *Eugenia jambos*, que forma bosques muy densos en isla San Cristóbal.

creciendo, dado que no existe un control eficiente de las introducciones. En este contexto es importante limitar el posible número de plantas ajenas que serán introducidas a Galápagos en el futuro, por medio de un mejor control. La dispersión entre islas debe ser controlada para evitar que *Rubus*, por ejemplo, sea llevada de San Cristóbal a Floreana.

Los problemas en las áreas silvestres van a seguir agravandose, hasta que radicalmente se enfrente el problema con mayores recursos económicos y humanos que sean canalizados a solucionar este problema prioritario. Para mayor efectividad de estos recursos se hace necesario un análisis profundo incluyendo estudios y acciones de manejo que ofrescan alternativas de solución.

Finalmente debido a que los problemas con plantas ajenas están relacionados con una falta de educación y apreciación de los valores naturales existentes en Galápagos una campaña de educación y extensión a la población humana es absolutamente necesaria para crear las bases y poder solucionar las problemas con organismos introducidos en general, y plantes en particular.

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MANAGING THE INVASIONS OF ALIEN UNGULATES AND PLANTS IN HAWAII'S NATURAL AREAS[1]

C. P. Stone[2] and R. A. Holt[3]

Abstract

Over ¼ of the state of Hawaii retains relatively intact natural biological communities. Most legally designated natural areas require active management to counter invasions by feral ungulates and alien plants. The three groups primarily involved in stewardship of natural areas in Hawaii are the state of Hawaii, which has responsibility for 315,419 hectares, including 18 areas totaling 43,841 hectares in the Natural Area Reserves System; The Nature Conservancy of Hawaii, with five preserves totaling 6,065 hectares; and the U.S. National Park Service, with two national parks totaling 104,426 hectares. Alien threats to different protected areas are addressed in different ways by the three groups—ranging from little or no management and research to active and integrated management and research programs. Management is also accomplished in different ways—ranging from volunteers to paid employees. The structure of the different groups varies from nearly all office personnel to nearly all field personnel, and development of stewardship programs is in different stages. Costs of programs per 100 hectares range from $114 to $1,758 (U.S.) for alien management and research, and 0–0.05 field personnel. Although none of the groups is effectively managing all alien invasions, considerable success has been possible when: (1) adequate planning and prioritizing of problems take place; (2) problems are managed in logical sequence (e.g., removal of ungulates prior to alien plant management); (3) research and management programs are well coordinated; (4) manageable areas are emphasized (e.g., fenced areas of a size commensurate with funding and available techniques); (5) responsible groups share information and other resources; (6) programs are adequately funded and continuous.

The introduction of alien biota to the Hawaiian archipelago began ca. 400 A.D. with the arrival of Polynesian voyagers from the Marquesas Islands, more than 4,000 km to the southeast (Kirch, 1985). In the 14 centuries before European arrival, at least four vertebrates of primary importance (pig, dog, chicken, rat) and ca. 30 introduced plants (Nagata, 1985) also entered the archipelago. Clearing, burning, agriculture, and hunting by Polynesian man were probably more detrimental to native ecosystems than were introduced alien forms during pre-European time.

With the arrival of the early European navigators in the 18th century, domesticated European pigs (*Sus scrofa*), goats (*Capra hircus*), cattle (*Bos taurus*), horses (*Equus caballus*), and sheep (*Ovis aries*) were introduced and encouraged (Tomich, 1986). Plants have also been brought in at an accelerated rate in the ca. 200 years since European arrival, and the increased opening of forests has allowed many species to naturalize. Of the approximately 4,600 alien plant species in the archipelago today, more than 600 have become established, and 86 (2%) are serious pests in native ecosystems (Smith, 1985).

The effects of Polynesian and continental people and their introductions on the Hawaiian biota have been severe. Although Hawaii includes only 0.2% of the land area in the United States, it accounts for 72% of the extinct birds in historical time and 37% of the federally listed endangered and threatened birds. For plants, about 30% of candidate species and 13% of federally listed species in the U.S., and 63% of the total known extinctions, are from Hawaii. Other forms, such as insects

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TABLE 1. Ownership of conservation lands in Hawaii.[1]

Landowners	Hectares	Percentages of state area
State of Hawaii		
Conservation subzone (protected)	236,345	14.6
Natural Area Reserves	43,841	2.7
Kaua'i Alaka'i Swamp	4,022	0.2
Plant, animal, or aquatic sanctuaries	31,211	1.9
Total	315,419	19.5
U.S. National Park Service	104,426	6.5
The Nature Conservancy of Hawaii	5,565	0.3
U.S. Fish and Wildlife Service[2]	1,287	0.1
U.S. Department of Defense	245	0.01
Totals	426,942	26.3

[1]Adapted from Holt & Fox (1985). Small privately protected areas, state and county parks, portions of state forest reserves not in the conservation subzone, and National Historic parks are excluded.

[2]5,360 hectares have been added to this to date in the Hakalau National Wildlife Refuge on Hawaii Island.

and mollusks, are too poorly known to make such comparisons but undoubtedly have been similarly affected. Eighty-five of approximately 150 identified natural community types in Hawaii (57%) are considered critically endangered. Yet over a quarter of the state still retains relatively intact natural communities.

Organization and Missions of Three Land Management Groups

Land ownership in Hawaii represents a mixture of private, state, and federal objectives, including conservation of natural areas. Federal, state, and county governments own nearly half of Hawaii's 1.6 million hectares. Major owners of lands dedicated to conservation (at least on paper) are shown in Table 1. Focus in this paper will be on three leading groups in terms of land holdings and/or active programs to manage Hawaii's diverse natural areas—the state of Hawaii, The Nature Conservancy of Hawaii, and the U.S. National Park Service. The State Natural Area Reserves System is emphasized because the goal is native ecosystem preservation. (Other state lands are managed for other purposes.) Management and research programs for alien plants and animals are emphasized herein, although protection from other threats as well as providing recreational opportunities and public education are sometimes difficult to separate from these programs.

Natural Area Reserves System

The Hawaii Natural Area Reserves System (NARS) was established by Hawaii statute in 1970 to "preserve in perpetuity specified land and water areas which support communities, as relatively unmodified as possible, of the natural flora and fauna, as well as geological sites, of Hawaii." An eleven-member Natural Area Reserves Commission (NARC), appointed by the governor of Hawaii and part of the Hawaii Department of Land and Natural Resources (DLNR) (which is the major state land management agency), recommends to DLNR and the governor areas for inclusion; recommends policies on controls and uses of NARS areas; advises on preservation of natural areas; and develops ways to extend and strengthen established natural areas (Tanimoto & Char, in press). The governor must approve the nominations for inclusion by executive order. Once an area is thus

TABLE 2. Areas included in State of Hawaii Natural Area Reserve System (NARS).[1]

Natural Area Reserves	Hectares	Primary ecological features
Hawaii Island		
Kahauale'a	6,769	'Ohi'a wet forest
Kipahoehoe	2,259	Mesic forest, 'ohi'a and koa wet forests
Laupahoehoe	3,195	'Ohi'a wet forest
Manuka	10,340	Dry and mesic forests, 'ohi'a wet forest
Mauna Kea Ice Age	1,576	Geological: Ice Age and Lake Waiau
Pu'u Maka'ala	4,899	'Ohi'a and koa wet forests
Pu'u o 'Umi	4,121	'Ohi'a wet forest, montane bog, headwaters of six perennial streams
Waiakea 1942 Lava Flow	259	Developing wet forest
Maui Island		
'Ahihi-Kina'u	501 (land) 327 (water)	Anchialine pools, last lava flow on Maui Marine ecosystem
Hanawi	3,035	'Ohi'a wet forest, cloud forest, alpine grassland
West Maui		
Kahakuloa Section	1,325	Pili grassland, mesic forests, cloud forests, 'ohi'a wet forests, montane bogs, headwaters and upper reaches of four perennial streams
Honokowai Section	304	
Pana'ewa Section	695	
Lihau Section	389	
Moloka'i Island		
Oloku'i	ca. 656	Mesic forest, wet shrub, and 'ohi'a wet forest
Pu'u Ali'i	538	Wet shrub and 'ohi'a wet forest
O'ahu Island		
Ka'ena Point	ca. 5	Coastal dune ecosystem
Mt. Ka'ala	445	Mesic and cloud forests, montane bog
Pahole	266	Dry and mesic forests
Kaua'i Island		
Hono o Na Pali	1,275	Mesic forest, 'ohi'a wet forest
Ku'ia	662	Dry and mesic forests
Total	43,841	

[1]As of June 1986.

included in the system, removal (except through trade for another area) is also through executive order. NARS now includes 18 reserves totaling 43,841 hectares on five islands (Table 2).

THE NATURE CONSERVANCY OF HAWAII

The Nature Conservancy of Hawaii (TNCH) was founded in 1980 as an affiliate of a nationwide, nonprofit conservation organization which had its beginnings in 1917 (Burnham, 1986). The mission of the national and Hawaii groups is "to find, protect, and maintain the best examples of communities, ecosystems, and endangered species in the natural world" (The Nature Conservancy, 1987). Through conventional real estate negotiations and innovative practices, such as "conservation easements" (paying landowners for allowing use of their land for conservation), TNCH acquires key Hawaiian natural areas. An important part of the strategy is a businesslike approach to conservation and a noncontroversial political style intended to foster cooperation among agencies, landowners, and others for conservation purposes. Volunteers play a big part in TNCH, from office

TABLE 3. Preserves currently owned by The Nature Conservancy of Hawaii and managed as natural areas.[1]

Preserve	Hectares	Primary ecological features
Moloka'i Island		
Kamakou	1,123	Rainforest, mesic forest, and shrubland
Pelekunu	2,237	Stream and rainforest
Maui Island		
Waikamoi	2,117	Rainforest and subalpine scrub
Kaua'i Island		
Kaluahonu	88	Seabird nesting site
Totals	5,565	

[1]Kipahulu lands (202 hectares) on Maui are not included because they are managed as open space. Lands serve as buffer to HALE.

and field workers to a Board of Trustees comprised largely of influential business people and a Scientific Advisory Committee comprised of university, state, private, and federal scientists.

Because choosing "the best examples" for land acquisition necessitates a comprehensive data base, TNCH has created the Hawaii Heritage Program (HHP), a sophisticated inventory and retrieval system for rare plants, animals, and communities. The HHP has inventoried about 10% of the state through review of publications and reports, personal interviews, and limited fieldwork.

Nationwide, the Conservancy has often donated or sold acquired lands to state or federal agencies for management. While such transfers of land have occurred in Hawaii, the Conservancy aims toward much more management of Hawaiian areas by the organization itself. TNCH now manages five preserves (Table 3) on three islands (6,065 hectares).

NATIONAL PARK SERVICE

Hawaii National Park was established in 1916 by the United States Congress. In 1961, Congress separated the established area into Haleakala National Park (HALE) on the island of Maui and Hawaii Volcanoes National Park (HAVO) on the island of Hawaii. Haleakala includes 11,462 hectares, and Hawaii Volcanoes contains 92,964 hectares; 87% of HALE and 57% of HAVO are congressionally designated wilderness areas, and both areas are International Biosphere reserves. HAVO has also received World Heritage designation.

The National Park Service (NPS) manages both of these natural parks to preserve outstanding scenic, geological, and biological values, and to ensure their availability for public use and enjoyment to the extent compatible with resource preservation. (NPS historic areas are also located in Hawaii and have different primary management goals, although natural resource conservation is required.) Prevention of deterioration in still largely native areas and reestablishment of ecosystems that would have existed without interference by contemporary humans are goals of NPS. Restoration to probable pre-European ecosystems is a goal in Hawaii parks (National Park Service, 1985).

UNGULATE AND ALIEN PLANT PROBLEMS AND PROGRAMS

NATURAL AREA RESERVES SYSTEM (NARS)

Management of alien species in the state NARS began on two O'ahu reserves in 1986 with the gathering of baseline information (Tanimoto & Char, in press). The effort lasted only three months

because of funding constraints. Native plants were inventoried, and alien plants were placed in one of three categories: major threats, plants to be monitored, or incipient threats. On the 445-hectare Mt. Ka'ala Reserve, *Rubus penetrans* (blackberry) was identified as the major threat because it is actively displacing native plant communities, especially along roadsides and in disturbed areas. On Pahole Reserve (266 hectares), *Schinus terebinthifolius* (Christmas berry), *Psidium guajava* (common guava), *P. cattleianum* (strawberry guava), and *Lantana camara* (lantana) were found to be major threats to the mesic forest. *Syzygium cumini* (Java plum), *Psidium guajava*, and *Schinus terebinthifolius* are major threats to the dry forest. Feral pigs are chief dispersers of the two guava species on Pahole Reserve; the Japanese white-eye (*Zosterops japonica*) is primarily responsible for the spread of *Schinus;* and increasing numbers of red-vented bulbuls (*Pycnonotus cafer*) also hasten *Schinus* dispersal (Tanimoto & Char, in press). Although hunting feral pigs is allowed, eradication seems necessary. Fencing to prevent pig access from adjacent areas is needed, but hunters object.

THE NATURE CONSERVANCY OF HAWAII (TNCH)

Three of the five TNCH natural area preserves in Hawaii are managed for alien plants and animals. One of these is Kaluahonu, on Kaua'i Island, a seabird nesting site monitored for weeds, feral pigs, and predators; it will not be discussed here. Another is open space and pastureland at Kipahulu, on Maui Island; native terrestrial communities are not present, so no ungulate or weed control programs are required there.

Kamakou and Pelekunu preserves. On the 1,123-hectare Kamakou Preserve on Moloka'i, reduction of damage by feral pigs and goats and axis deer (*Axis axis*) to a level that prevents degradation of the forest is emphasized. Pigs are the greatest threat, particularly in the rainforest; the approach has been to use experimental barrier fencing and hunting in nine management areas defined largely by topography and accessibility. Year-round public hunting without bag limits has reduced pig disturbance in accessible portions of the preserve. Remote areas cannot be covered easily on one-day hunts, and abundant animals outside of the preserve have no barrier to invasion. Hunts by staff have supplemented public hunting. Monitoring indicates that approximately 64 hunts per year for pigs probably prevent population increase. Public hunting has helped keep deer and goat populations small.

Alien plant control programs emphasize: (1) species that invade ecosystems even in the absence of disturbance; (2) species for which safe and effective control methods are available; and (3) species with limited distributions. A point system using these criteria ranks existing weeds. Research is encouraged for invasive plants lacking adequate control methods. Some experimental herbicide work is being conducted by University of Hawaii personnel (Motooka, this volume).

Manual weed control is accomplished largely by volunteers under the direction of the preserve manager. Serious problems include *Rubus penetrans*, *Grevillea robusta* (silk-oak), *Acacia decurrens* (black wattle), *Corynocarpis laevigata* (karaka nut), *Psidium cattleianum*, *Melaleuca leucadendra* (paperbark), *Hedychium coronarium* (white ginger), *Pinus* spp., and *Fraxinus uhdei* (tropical ash). Mechanical treatment (cutting, girdling, or pulling) and application of glyphosate (Roundup) are the primary control methods.

Ungulate and weed control programs at the newly acquired Pelekunu Preserve (2,327 hectares) on Moloka'i Island are in the planning stages, with fieldwork initiated during the summer of 1987. A second full-time staff member was added on Moloka'i to support the expanded field program there.

Waikamoi Preserve. On the 2,117-hectare Waikamoi Preserve on Maui, fence construction to exclude feral cattle, pigs, goats, and axis deer has been a major priority. The shape of the preserve results in considerable exposed boundary, but fortunately the south boundary abuts Haleakala

National Park, which has now been fenced. The TNCH fence along the preserve's western boundary, vulnerable to cattle and pigs, has also been complete. Six ungulate control units have been established, based largely on topography and accessibility, and fencing of most of these units is planned in the next few years. Public and TNCH staff hunts are conducted for pigs and goats in three remote units, and preserve staff and Haleakala Ranch Hunting Club members and guests hunt in three more accessible units. Pig control by traps, barrier fences, and snares is under way.

Alien plants have been ranked with the same system used on Kamakou Preserve. Important species include: *Rubus penetrans, Ulex europaeus* (gorse), *Acacia decurrens, Andropogon virginicus* (broom-sedge), and *Pennisetum clandestinum* (kikuyugrass). There is considerable concern about *Passiflora mollissima* (banana poka), which, although not in the preserve, is found nearby (within 8 km). This plant has the potential of overwhelming the native koa-'ohi'a (*Acacia koa–Metrosideros polymorpha*) forest, which is habitat for the endangered birds for which the preserve was created.

NATIONAL PARK SERVICE (NPS)

Haleakala National Park. Fence maintenance and feral goat and pig control are top priorities in a 6,920-hectare subalpine area (Crater District) in this park. Fence construction in a 4,542-hectare rainforest area (Kipahulu District) and development of feral pig control methods there are next in priority. The Crater District is now fenced with 51 km of galvanized woven wire fence 120 cm high, with one strand of barbed wire at ground surface and two above the woven wire. Goat and pig control are proceeding rapidly in this fairly open subalpine area. Fewer than 400 goats are thought to be present in the Crater District (R. Nagata, pers. comm.). A few feral pigs remain inside the fence. Control of pigs is conducted by hunting from helicopter, on horseback, and on foot. Organized volunteer and staff hunts at approximately one-month intervals are used.

Nearly 14.5 km of galvanized woven wire fence (120 cm) with one strand of barbed wire at ground surface across Kipahulu Valley in native rainforest are now completed. Feral pig control techniques being tested include trapping, baiting, and snaring. Use of toxicants may be necessary for elimination of the last pigs. Most emphasis has been on snaring pigs in this remote area. To date, 1,670 multistrand wire snares have been set in the fenced 2,340-hectare study area. One hundred fifty-six animals have been taken in a 14-month period, but pig recruitment may be compensating for removal.

Loope et al. (in press) ranked *Psidium cattleianum, Clidemia hirta* (Koster's curse), *Passiflora mollissima,* and *Pennisetum setaceum* (fountain grass) (the last three not yet in the park) as top threats to Haleakala ecosystems. Loope et al. (in press) listed existing problems according to major ecosystems (Table 4). Recommended management actions for the Crater District include control of *Ulex europaeus, Cirsium vulgare* (bull thistle), *Rubus penetrans, Pinus* spp., and *Eucalyptus* spp., and monitoring of the response of selected aliens to goat removal. Strategic control of plants such as *Pennisetum clandestinum, Ricinus communis* (castor bean), *Lantana camara,* and *Psidium guajava* may be necessary where rare plants are threatened. New aliens should be monitored and removed.

In the Kipahulu District, the main alien plant is *Psidium cattleianum.* Herbicidal control with outlying populations is being tested. *Clidemia hirta* and *Passiflora mollissima* are major potential threats but are not yet in Kipahulu Valley. Numerous aggressive species threaten to invade the upper valley. These include *Bambusa* sp. (bamboo), *Syzygium jambos* (rose apple), *Psidium guajava, Schinus terebinthifolius,* and *Melaleuca leucadendra.* Beyond effective control are *Paspalum conjugatum* (Hilo grass), *Rubus roseifolius* (thimbleberry), and *Eupatorium adenophorum* (white thoroughwort).

Planned management actions after removal of pigs in Kipahulu Valley include controlling *Psidium cattleianum* with chemical and mechanical means in the upper part of its range, and control of other selected aliens if this species can be controlled.

TABLE 4. Major near-native ecosystems in Haleakala National Park.[1]

Ecosystems	Dominant or important native plants	Major alien plant problems
Alpine desert	*Argyroxiphium sandwicense*	None at present
Subalpine grassland	*Deschampsia australis*	*Holcus lanatus*, *Rubus penetrans*
Subalpine shrubland	*Styphelia tameiameiae*, *Coprosma* spp., *Sophora chrysophylla*	*Holcus lanatus*, *Anthoxanthum odoratum*, *Pinus* spp.
'Ohi'a-dominated rainforest	*Metrosideros polymorpha*	*Rubus penetrans*
Koa-dominated rainforest	*Acacia koa*	*Psidium cattleianum*, *Paspalum conjugatum*
Montane bog	*Oreobolus furcatus*, *Carex svenonis*, *Argyroxiphium grayanum*	*Holcus lanatus*, *Sacciolepis indica*
Dryland forest and shrubland	*Dodonaea eriocarpa*, *Osteomeles anthyllidifolia*, *Styphelia tameiameiae*, *Santalum haleakalae*	*Pennisetum clandestinum*, *Holcus lanatus*, *Eupatorium adenophorum*

[1]Adapted from Loope et al. (in press).

Hawaii Volcanoes National Park. Goat and pig fence construction, control of feral pigs in newly fenced units, and maintenance of goat and pig fences are the top three priorities in this park. Elimination of remnant pigs and feral goats at high elevations is next in priority. Feral pig control in HAVO is conducted in 140–1,900-hectare units fenced with 81-cm woven wire with one strand of barbed wire at ground level. Hunting with dogs has been the most effective method for removing initial populations (Stone & Keith, 1985). Baiting and snaring may prove most effective for remnant populations.

Feral goats have been largely eliminated from the lowlands by fencing park boundaries, constructing barrier fences within the park, and using organized hunts by park staff (Baker & Reeser, 1972). A "Judas goat" program utilizing radio-collared animals that lead hunters to remaining herds has been successful in removing the last few animals (Katahira & Stone, 1982). In the sparsely vegetated upland portions of the park (above 2,030 m) goats have access from adjacent ranchlands because boundaries have not been fenced. About 20 animals usually reside in the park and will be removed as funds allow.

Delineation, study, and management of Special Ecological Areas (SEAs) are important emphases in HAVO. SEAs (Table 5) are chosen for emphasis because they are still largely intact, represent important ecosystems, contain rare and/or diverse components, are manageable, and can be interpreted readily for the public (Tunison & Stone, in press). One of the major reasons for emphasis on this program, rather than individual alien plant species, is the realization that parkwide control of widespread alien species is not feasible with current or expected staffing and funding. For example, estimates for parkwide control of *Pennisetum setaceum*, over 8,000 hectares, were ca. 1,500 worker-days per year (Tunison, in press).

Alien plants currently being controlled in SEAs include *Myrica faya* (firetree), *Psidium cattleianum*, *Hedychium gardnerianum* (kahili ginger), *Linociera ligustrina* (Russian-olive), and *Tropaeolum majus* (nasturtium). *Hedychium* is controlled in most areas by manual removal. Picloram has been used on *Hedychium*, *Myrica*, *Psidium*, and *Linociera* (pellets for the first, and cut stump treatments for the last three species). Further testing may pinpoint a substitute for this chemical, which may become unavailable in the future in Hawaii. Triclopyr (GARLON 4) has been effective on *Tropaeolum*, but its seed banks are large and persistent.

Approximately 475 non-native plant species occur in HAVO, and at least 40 of these invade native ecosystems. Although alien plant management in SEAs is now emphasized, control of highly

TABLE 5. Ecological zone, vegetation type, size, and alien plant threats to Special Ecological Areas (SEAs), Hawaii Volcanoes National Park.

Ecological zones	Vegetation types	Hectares	Weed problems	Names of SEAs
Coastal lowland	Pili grassland	200	Not known	Holei
		300	*Pennisetum setaceum* *Hyparrhenia rufa*	Ka'aha
	Strand	50	None	Apua Point
	Native scrub, dry forest, mesic forest	300	*Psidium cattleianum* *Schinus terebinthifolius*	Kamoamoa
Submontane seasonal	Dry 'ohi'a woodland/scrub	12	*Myrica faya* *Linociera ligustrina* *Psidium cattleianum*	Ainahou North
	Dry 'ohi'a woodland	33	*Myrica faya* *Linociera ligustrina*	Ainahou South
	Dry 'ohi'a scrub	2,700	*Myrica faya* *Grevillea robusta* *Pennisetum setaceum*	Keamoku
		280	*Myrica faya*	Kipuka Kahali'i
	Dry lama forest	50	*Lantana camara*	Naulu
	Sparse (thermal)	5	None	Puhimau
Montane rainforest	Hapu'u/'ohi'a	280	*Passiflora mollissima*	'Ola'a (large tract)
		140	*Passiflora mollissima* *Hedychium gardnerianum* *Rubus ellipticus*	'Ola'a (small tract)
	'Ohi'a/Hapu'u	10	*Myrica faya* *Psidium cattleianum* *Hedychium gardnerianum*	Thurston
Montane seasonal	Mesic 'ohi'a/ soapberry forest	30	*Hedychium gardnerianum* *Psidium cattleianum* *Tropaeolum majus* *Solonum pseudocapsicum*	Kipuka Puaulu
		560	*Myrica faya*	(Buffer zone)
	Mesic koa/'ohi'a soapberry forest	50	*Solanum pseudocapsicum*	Kipuka Ki
	Mountain parkland	3,300	*Rubus penetrans* *Holcus lanatus* *Paspalum spp.* *Microlaena stipoides* *Andropogon glomeratus*	Mauna Loa
	Subalpine	1,000		Mauna Loa
	Alpine	1,000		Mauna Loa
Montane seasonal	Native ferns	ca. 10	*Myrica faya* *Psidium cattleianum*	Steam Banks
Submontane seasonal	Mesic 'ohi'a forest	ca. 250	*Myrica faya*	Keanakako'i
Submontane seasonal	Dry 'ohi'a	ca. 200	*Pennisetum setaceum*	Poliokeawe
Submontane rainforest	'Ohi'a/hapu'u forest	ca.2	*Myrica faya* *Psidium cattleianum* *Paspalum conjugatum*	Napau Pit Craters
Submontane rainforest	'Ohi'a/hapu'u forest, various seral stages of primary succession on lava	1,500–2,000	*Psidium cattleianum* Alien grasses	East Rift Kipukas and lava flows
Coastal lowland Ka'u desert	Grassland with native shrubs	ca. 300	*Pennisetum setaceum*	Kukalau'ula
	Dry 'ohi'a scrub	ca. 300	*Pennisetum setaceum*	Yellow Cone

TABLE 6. Economics and effort in managing natural areas in Hawaii.

Group	Area managed (hectares)	Numbers of resource management/ research staff, 1987		Annual amounts spent in 1987 on resource management/research	
		Permanent	Total	Total ($ U.S.)	Per 100 hectares ($ U.S.)
State of Hawaii (Natural Area Reserves)	43,841	2	2	50,000[1]	114
The Nature Conservancy	5,565	4.5	4.5	165,000[2]	2,964[4]
National Park Service	104,426	15	39	1,836,000[3]	1,758
Totals and Means	153,832	21.5	45.5	2,051,000	1,333[5]

[1]Estimate $250,000/year in 1988 ($570/100 hectares). At present no persons in field.

[2]Estimate $261,000/year in 1988 ($4,690/100 hectares). At present three persons in field. Includes public education programs.

[3]At present all persons in field at least part time. Includes fencing costs.

[4]40% ($66,000 or $1,186/100 hectare) being used for direct ungulate and alien plant control or research at present.

[5]Mean is $1,269/100 hectare if only TNCH alien plant and animal control and research expenses ($66,000) are included.

localized species is also currently being conducted parkwide. Fire control, management of alien plants after ungulate removal, and restoration of native plants where seed sources no longer exist are also necessary components of plant management programs.

A preliminary, modest plant-control research program based at HAVO has produced safe, cost-effective herbicidal control methods for five alien species in near-native ecosystems (Santos et al. 1986). Emphasis of future research in the next 3–5 years will include: integration of herbicidal and other control methods; evaluation of retreatment protocols; long-term monitoring of effects on native and alien plant species and communities; testing of new herbicides and application techniques; studies of alien plant phenology and ecology; and testing of chemicals in different climatic, edaphic, and ecological conditions. Control method research will initially emphasize *Myrica faya*, *Psidium cattleianum*, *Passiflora mollissima*, *Tropaeolum majus*, *Rubus ellipticus* (Himalayan yellow raspberry), *R. penetrans*, and *Hedychium gardnerianum*; work will be focused on SEAs.

Economics and Effort

A comparison of costs and manpower used to manage near-natural areas in Hawaii is presented in Table 6. Of the groups actively managing natural areas, only NPS supports its own integrated research effort in Hawaii, and costs for this are included in the table. The HHP of TNCH provides an important data base for the Conservancy and other groups. However, that information is currently used largely to select new areas for acquisition rather than to manage already acquired areas; thus, costs for HHP are not included in the table. At present DLNR has no in-house research capability to support NARS.

Staffing for the NARS program in 1987 included an executive secretary and a half-time clerk typist. The budget was $50,000. Two temporary biologists were hired in 1986 for three months, but funding was not continued. Funding at $250,000 per year was expected for 1988, and additional funds are expected to be available to support planning and to build data bases for future NARS designations. Because there is no NARS management staff, state-owned areas identified as exemplary paradoxically receive less attention than other state-owned conservation lands managed as forest reserves or wildlife sanctuaries in Hawaii.

Staffing for TNCH preserve management now includes four and one-half persons: a full-time preserve manager on Moloka'i; another with an assistant on Maui; and one and one-half people in Honolulu, including a director of science and stewardship and a half-time administrative assistant. Out of a budget of $165,000 for 1987, about 40% ($66,000) is used on feral ungulate and alien plant programs. TNCH has no research capability, and fence building is emphasized on one preserve only. A nationwide strategy of the Conservancy has been to donate or sell acquired lands to state or federal agencies for management. In contrast to this, TNCH is now embarking on a course of action that will result in much more management by the organization itself. Management of the four existing natural area preserves on three islands is projected to require $261,000 in 1988. The Conservancy is building a "stewardship endowment" from private donations, the investment income from which is targeted to support the majority of annual preserve operational costs. While fund-raising has been successful, considerable progress is needed before stewardship funding is secure and adequate.

Appropriations for natural resource management in the two national parks are long- and short-term. Long-term budgets for natural resource management are approximately $300,000 for Hawaii Volcanoes and $150,000 for Haleakala. However, both parks have had additional large, short-term appropriations for fence building, ungulate management, and alien plant control in recent years. Fence maintenance costs $27,000 per year in HALE and $47,500 at HAVO. In 1987 the HALE resource management budget was $1,045,000, and the HAVO budget was $347,500. Long-term total park budgets for 1987 (for all park functions) were $1,095,400 for HALE and $1,943,100 for HAVO.

Funding for research in the parks has similarly been enhanced to deal with critical problems in amounts up to $100,000 per year for as long as three years. Long-term research programs are supported at a $100,000 per annum level in HALE and at about $130,000 in HAVO. Research budgets in fiscal year 1987 are $118,000 for HALE and $325,500 for HAVO. NPS supports one research and nine permanent resource management positions in HAVO, and one research and two permanent resource management positions in HALE. In addition, NPS supports two scientists in Honolulu. These individuals are involved in research on biocontrol of alien plants and provide research program assistance and program overview. Their combined budget is $177,000. Temporary research personnel are continually part of the research staffs of both parks, and volunteers are often used. The two parks together have 37 paid staff members (plus the two Honolulu-based scientists) involved in resource management and research; most of these are field personnel.

Concluding Remarks

The overwhelming problem of managing alien plants and animals in Hawaii is approached differently by different land management groups. Although the three groups contrasted herein are at different stages in the management progression (NPS most advanced, NARS least), some conclusions are possible. Success in solving problems has been demonstrated (by NPS, TNCH, and NARS to a limited extent) when small near-native areas or portions of reserves are the focus. Emphasis on sequential steps (as demonstrated by NPS and TNCH), including problem analysis and prioritization, data base organization and accumulation, fencing, ungulate removal, and invasive alien plant management, is also critical. NPS and TNCH emphasize monitoring of management activities and feedback from it to improve approaches. Integration of efforts by research and management at each stage (by NPS), and coordination among different land management groups (by NPS and TNCH) have promoted progress.

A more focused emphasis on conservation biology in Hawaii (irrespective of land ownership) is overdue. This should include a strong conservation education thrust and considerable long-term research on ecosystem components, properties, and processes. However, enduring commitments to adequate, long-term alien plant and animal management are also critical. The support level required

varies with the management progression (e.g., fence building and fact-finding are very expensive for a time), but continuity of support is needed to retain experienced people, make progress over significant land area, and preclude reversal of alien control efforts. It is likely that stewardship of near-native lands in Hawaii will require more active and intensive efforts by all management groups in the future.

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WEED MANAGEMENT IN HAWAII'S NATIONAL PARKS[1]

Clifford W. Smith[2]

Abstract

Eight hundred sixty alien species have naturalized in Hawaii. Ten percent of them are serious threats to native ecosystems. Many of these species are in the national parks. Priorities for dealing with them have been established dependent on their distributions, disruptions of the ecosystem, and controlabilities. Manual and ecological weed control techniques have limited application. Chemical control is used extensively but many herbicides are banned from use in parks. An interagency biocontrol program has been established to evaluate some potential control agents. A leaf-eating insect has just been approved for release against one of the most serious weeds, *Passiflora mollissima*. Education (particularly of administrators but also the general public), adequate documentation of weeds in native ecosystems, research on species to predict their invasiveness, and better control measures are all necessary in order to prevent new weed disruptions in Hawaii's national parks.

The Hawaiian archipelago, isolated from the nearest continental landmass by at least 2,000 miles, is well known for its high levels of endemism (Carlquist, 1980). The natural rate of establishment of species in the islands is very low (Table 1). The precontact Hawaiians introduced few plants that naturalized. Since 1778, the status of the Hawaiian flora has changed (Table 2) and the rates of establishment increased dramatically. Today, native and naturalized species of angiosperms are almost equal in number. It is conservatively estimated that there are a further 4,000 species introduced to gardens and arboreta or for agriculture. Eighty-six of the 860 naturalized species are serious pests in native ecosystems and a further 34 are potentially so (Smith, 1985). Gymnosperms, previously absent, are now established, and naturalized aliens from other groups (other than lichens) are present.

The impact of the aboriginal Hawaiians on the native ecosystems, particularly the lowlands, was devastating (Kirch, 1982; Olson & James, 1982; Stone, 1985). However, those impacts together with violent storms, floods, and lava flows have been greatly exceeded since 1778. Wetlands have been drained, forests have been cleared, and domesticated ungulates have been allowed to run feral. Native animals and plants have been ravaged by alien diseases and predators. Alien plants have had a significant negative impact, which Vitousek (1986) noted to be as stong as impact from alien animals. The disturbance is so pervasive that very few areas not influenced by alien ecological factors remain (Smith, 1985). The resource manager of natural areas has to contend with all of these factors. This paper discusses the alien plant management program in Hawaiian national parks.

Hawaii's National Parks

There are seven units of the National Park Service (NPS) in the Hawaiian Islands (Fig. 1; Table 3). Haleakala and Hawaii Volcanoes are the largest parks and possess a great diversity of resources; both are biosphere reserves and have been nominated as world heritage sites, as has Puuhonua o

[1]My thanks to L. L. Loope, C. P. Stone, D. Taylor, and T. Tunison for comments on an earlier draft of this paper. Part of the work was supported under a cooperative agreement (CA8016 2 0001) between the University of Hawaii and the National Park Service.

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TABLE 1. Calculated rates of successful introductions (years/species) of eucaryotic plants to the Hawaiian Islands.

	Naturally	By Polynesians	Since 1778
Angiosperms	72,727	72	0.24
Gymnosperms	0	0	52
Pteridophytes	153,846	0	8
Bryophytes	85,837	0	16
Lichens	28,531	0	0
Algae	66,667	0	5

TABLE 2. Numbers of successful establishments of eucaryotic plants to the Hawaiian Islands.

	Naturally	By Polynesians	Since 1778
Angiosperms	275	25	860
Gymnosperms	0	0	40?
Ferns	130	0	25
Bryophytes	233	0	13
Lichens	701	0	0
Algae	300	0	40

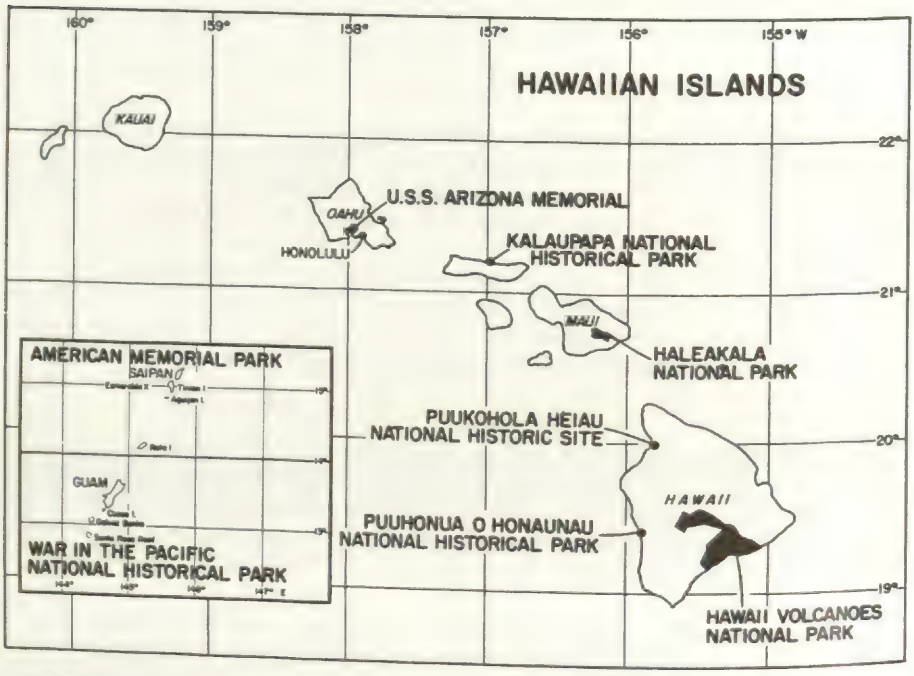

FIGURE 1. Map showing the locations of the U.S. national parks in the Pacific.

TABLE 3. The areas, elevation ranges (m), presence vs. absence of endangered species and visitor counts in 1986 of the seven units of the National Park Service in Hawaii.

Parks	Areas (ha)	Elevations (m)	Endangered species	Numbers of visitors
Kaloko-Honokohau National Historical Park	520	18	Yes	0
Kalaupapa National Historical Park	4,361	1,267	Yes	12,775
Haleakala National Park	10,940	3,007	Yes	1,304,330
Hawaii Volcanoes National Park	87,807	4,104	Yes	1,507,242
Puukohola Heiau National Historic Site	14	48	Yes	56,424
Puuhonua o Honaunau National Historical Park	72	22	No	432,400
U.S. Arizona Memorial	5	6	No	1,435,885

Honaunau. The historical parks also have significant natural resources, including endangered species, mostly birds. All parks, with the exception of the recently established Koloko-Honokohau, have visitor management problems.

Overview of NPS Resource Management Planning

The national parks in the United States were established to preserve resources for future generations as well as make them accessible to people today. Conservation has been a dominant philosophy. However, by 1961 it had become apparent that there were some serious problems. A blue-ribbon panel (Leopold et al., 1963) castigated NPS on its research and resource management in terms of effort and concepts. At about the same time, the provisions of the National Environmental Protection Act essentially required the development of a general management plan for each park. Resource management plans were then developed in which major problems were identified and discussed, and strategies were developed to resolve them. In Hawaii, control of alien species has always been a high priority in all parks.

More recently, NPS has gone through two exercises identifying threats. The most recent, the Natural Resource Assessment and Action Program, was quite systematic. Seven categories of threat were identified: construction and operation of structures and facilities; water supply and control activities; agricultural and silvicultural activities; mining and minerals activities; visitor activities, including waste disposal and resource contamination; physical processes; and biological processes. From this analysis, each park came up with a list, in priority order, of its resource management and related research needs. Feral animal and alien plant control were top priority issues in Western Region parks but basic inventory and ecological research were also very high. Systematic evaluations of this type help identify problems, evaluate remedies, plan strategies, and develop budgets and funding requests.

The Management Dilemma

Hawaii is perceived by many people as a paradise, though some consider it to be "paradise lost." It is the center for a large tourist industry (5.6 million visitors in 1986), which demands extensive developments in lowland areas and landscaping with "exotic" plants. It is the center of an agricultural industry using vast tracts of land and large quantities of water. The extensive military operations import and export large quantities of material. The resident inhabitants (1,062,344 in 1986) also bring in many items to enhance their lives. The pressures on the political system to support, endorse, or tolerate many activities that are detrimental to the native ecosystems and species are enormous.

TABLE 4. The twelve worst weeds in Hawaiian national parks. Park abbreviations: KAHO—Kaloko-Honokohau National Historical Park, KALA—Kalaupapa National Historical Park, HALE—Haleakala National Park, HAVO—Hawaii Volcanoes National Park, PUHE—Puukohola Heiau National Historic Site, PUHO—Puuhonua o Honaunau National Historical Park. Park names in parentheses indicate that the weed is not yet in the park but is close to the boundary.

Andropogon virginicus	KALA, HALE, HAVO, PUHE, PUHO
Clidemia hirta	KALA, (HALE, HAVO)
Lantana camara	KAHO, KALA, HAVO
Leucaena leucocephala	KAHO, KALA, HAVO, PUHO
Melinis minutiflora	KALA, HALE, HAVO
Myrica faya	HAVO, (HALE)
Passiflora mollissima	KALA, HALE, HAVO
Pennisetum clandestinum	KALA, HALE, HAVO
Pennisetum setaceum	KAHO, HAVO, PUHO, (HALE)
Psidium cattleianum	KALA, HALE, HAVO
Rubus argutus	KALA, HALE, HAVO
Schinus terebinthifolius	KAHO, KALA, HALE, HAVO, PUHO

Weed management in Hawaii, as in most parts of the world, has concentrated on agricultural problems; the worst weeds are deemed "noxious." Recent attempts in Hawaii have tried to make the list more comprehensive, which presents problems because it has become cumbersome and controversial. Yet, listing has some definite advantages by prohibiting importation, focusing managers' attentions on these species, frequently raising a weed's position on priority lists, making control mandatory, and directing funding toward sometimes controlling species.

Animal, plant, and soil importations are controlled only in so far as they will affect crops and other farming interests even though regulations are normally written more broadly; the larger the potential economic impact, the more aggressive the control. In Hawaii, commercial ventures interested in diversifying agriculture and horticulture continue to import large numbers of species with only minor restrictions. Hawaii's botanic gardens also introduce enormous numbers of species, these sometimes hosting large numbers of epiphytes. For example, the Honolulu Botanic Gardens imported "well over 10,000 accessions" 1975–1985 (Weissich, 1984). The Pacific Tropical Botanical Garden is systematically establishing gene banks of several crop plants, e.g., *Artocarpus altilis* (breadfruit), as well as extensive collections of other genera, e.g., *Erythrina* (Theobald, 1982). Weissich (1984) suggested that Hawaii should become an "alternate site" for many of the tropical rainforest species that are now disappearing under the axe. Needless to say, that idea met strong and immediate opposition (Gagné, 1986).

Twelve very troublesome weeds plague Hawaii's national parks (Table 4). Their impact on native ecosystems was discussed by Smith (1985), and five of them are also discussed by Mueller-Dombois & Loope (this volume). These species have very little in common. They come from a diversity of life forms, and their impact on native ecosystem properties varies considerably.

The management of alien plants in natural island ecosystems presents problems. New threats are always appearing, and the burgeoning human population continuously encroaches on the buffer zones around most parks. In contrast with agricultural crops for which all species other than the crop plant are controlled, in management of natural ecosystems generally only one species is controlled while other species are protected. All previously developed techniques are used but, because of the extreme selectivity necessary, integrated pest management is required. In many respects it is a very recent endeavor.

SETTING PRIORITIES

Setting priorities depends on a broad informational base. First, it is important that there is a complete inventory of the flora. Second, it is very useful to take each target species through an

integrated pest management evaluation (Olkowski & Olkowski, 1983). Third, the species need to be segregated into categories describing their potential for control. In Hawaii, we have found the following groupings useful: (1) Highly localized, potentially disruptive species. These are localized enough for herbicidal or manual control requiring modest manpower with consistent follow-up. (2) Established, disruptive species. These agressive weeds are well established but somewhat localized. Because they are more widespread than category 1 species, cost-effective control techniques are essential. (3) Candidates for biological control. These species are too widespread for conventional control measures. They were determined by Gardner & Davis (1982) as good candidates for biological control. (4) Candidates for control in part of their range. These highly disruptive species are too widespread to be controlled park-wide. However, their impact in special ecological areas is too significant to wait for biological control. (5) Species to be monitored. Their distributions and rates of spread need monitoring to determine the necessary management status.

Priorities are then set to conform with resources available to the manager. There are three principal sources of support: park base funding, special funding for specific projects, and volunteers. Park base funding is generally an assured source of funding, but it is fixed and subject to absorbing inflation. Special funding is very important because it is project-specific, but it requires special requests. Volunteers are normally available in most parks. Volunteer programs have two major drawbacks: they require substantial organization and the quality of workers is extremely variable. However, this latter approach has been used effectively in the national parks and The Nature Conservancy reserves in Hawaii (Holt, in press).

Feasibility is a very important part of the priority-setting process. Sometimes decisions have to await better data on the distribution of a species. Generally, one has to compromise between the severity of the problem and the ability to control. For example, fountain grass (*Pennisetum setaceum*) invaded Hawaii Volcanoes National Park in the early 1970s. Had it been controlled at that point a lot of money could have been saved. At present, the park has abandoned its ambition to eradicate fountain grass and now hopes to contain it below 1,300 m elevation (Tunison, in press).

MAPPING

One of the most important aids in establishing priorities, controlling, and monitoring weeds has been mapping their past and current distributions. Maps allow a manager to determine the scope of the control program and enable development of control strategies of predictable costs. Rates of spread are deduced from past records. Outlying populations are carefully identified since these are generally the primary targets in eradication strategies (Moody & Mack, 1988). Weed distributions are readily correlated with vegetation types (assuming a vegetation map exists), elevation, rainfall and temperature isohyets, and soil types. The weed's potential range is then evaluated, enabling establishment of priorities among various weeds. Graphical information of this type is extremely useful for determining the scope of a particular problem. Distribution maps are also useful, succinctly documenting a weed control program's status.

The mapping program in Hawaii, though not overly organized, has recorded the island-wide distribution of three of our most important forest weeds—*Passiflora mollissima* (Warshauer et al., 1983), *Clidemia hirta* (Wester & Wood, 1977; Smith, in press), and *Myrica faya* (Whiteaker & Gardner, 1985). Several other weeds are mapped on various islands.

Two approaches have been used. The first is to concentrate on one weed at a time and visit most known and potential localities. This approach is realistic and relatively inexpensive in Hawaii where many people have extensive field information. On confirmation, the weed's distribution is then mapped on the 1:24,000 orthoquad topographic maps. The map for *Myrica faya* cost less than $6,000 and for *Clidemia hirta*, less than $1,500.

The other approach, in which all plants are surveyed systematically, was used by the U.S. Fish and Wildlife Service Forest Bird Survey. They surveyed all major islands except Oahu by running

transects 3.2 km apart down through the forest from 2,250 m to 500 m (Scott et al., 1981). Each transect was sampled every 134 m. Notes were taken on when species first appeared and other unusual occurrences. Detailed vegetation maps were drawn using stereoscopic high-altitude photographs. Distribution maps of more widely distributed weeds have been produced using computer database management programs (Jacobi & Warshauer, in press). Recently established and occasionally recorded species are not readily amenable to this technique. This type of program is extremely expensive: the forest bird survey cost $875,000 with added costs from subsequent analysis.

Review of Past Work

Vitousek (1986) summarized the effects of alien plants on native ecosystems and noted that their impact is as severe as that of alien animals.

One could assume that the behavior of an introduced plant elsewhere would indicate its potential weediness in a new environment. Such an assumption can be deceptive especially in insular environments with their specialized and species-poor floras. Many niches appear to be unfilled, and invading species generally arrive without the predators and parasites that constrain them in their native environments. The resilience of the Hawaiian flora and ecosystems was thought to be very poor (Lyon, 1918, 1919; Degener, 1930). Recent evidence, however, suggests that if disturbance is eliminated then the local species are able to withstand invasions (Loope & Scowcroft, 1985; Mueller-Dombois, 1981). This change in attitude has given managers much greater hope of achieving their objective and resulted in a $10M research and resource management effort in Hawaii's national parks over the last 20 years.

A number of papers dealing with alien weed problems in Hawaiian ecosystems have appeared recently (Gardner & Davis, 1982; Gerrish & Mueller-Dombois, 1980; La Rosa, 1983; Mueller-Dombois, 1981; Smith, 1985; Sorenson, 1980; Warshauer et al., 1983; Wester & Wood, 1977). Research continues on various aspects of the biology of *Citharexylum spinosum, Clidemia hirta, Myrica faya, Rubus* spp., and *Ulex europaeus* in order to develop ways of countering these threats.

Understanding the historical perspective of land management is also important. The Hawaiians had a devastating impact on the lowland vegetation, but areas above 1,000 m were affected only marginally (Kirch, 1982; Olson & James, 1982). The impact of feral animals in historical times is poorly documented. The objective of NPS is to restore the ecological processes to those when Captain Cook first visited the islands in 1778. In many instances, even that objective is impossible because we have no knowledge of the ecosystem at that time, several native species are now extinct, and alien species now dominate.

Control Strategies

Five basic control strategies are used: manual, mechanical, ecological, chemical, and biological control.

Manual Control

Manual control is a good strategy for controlling outliers and confining species to certain areas. Its greatest use is in eradicating species as they become established in a natural area. This approach has been successful in Hawaiian parks to eliminate two *Atriplex* species, *Arthrostemma latifolia, Lupinus* species, *Melochia umbellata,* and *Ulex europaeus* (Tunison & Zimmer, in press). The technique is unsuitable for widely distributed weeds except in special cases because it is labor-intensive and native species are trampled. It has been effective against outliers of fountain grass in the coastal grassland of HAVO.

MECHANICAL CONTROL

This is not a suitable technique in natural areas except under certain unusual circumstances. For example, regeneration of a koa forest has been achieved by ground scarification in clear-cuts and following wildfire (Scowcroft & Wood, 1976).

ECOLOGICAL CONTROL

Ecological control is aesthetically attractive because it appears to be natural. The most obvious examples are when shrubs or trees are released from some constraint, such as feral animals, and shade out alien species, e.g., *Andropogon* species. Exclosure studies have demonstrated considerable potential in some areas for this approach (Loope & Scowcroft, 1985). Unfortunately, this strategy requires time and patience and is not considered suitable by managers who are goal-oriented in the short-term because their tenure is limited.

CHEMICAL CONTROL

Probably the most frequently used agent in weed management is herbicides. These are generally cheap and dramatically effective. However, well-known limitations and side effects have resulted in institutional bans. In management of native ecosystems these issues are compounded by the fact that managers generally try to control one species only, as opposed to agricultural programs where one is trying to control all species except one. The increased labor involved in applying the herbicide to one species can increase the cost dramatically.

Chemical control is the strategy of last resort in certain instances where biocontrol is not possible because of political conflicts, e.g., range grasses such as *Pennisetum clandestinum* and horticultural species such as *Hedychium gardnerianum*. Each target species has to be evaluated as to the best herbicide. The lowest effective concentration of each herbicide and its potential impact on native vegetation must be determined. Along these lines, NPS has an ongoing investigation in Hawaii that has cost $75,000 over the last three years and is anticipated to cost approximately $34,000 for the next three years. Part of the expense is evaluating new herbicides because previously used chemicals are forbidden for use in parks due to potential long-term damage. However, the bulk of the expense is due to development of efficient application techniques that minimize the delivery of chemicals to nontarget species (Santos et al., 1986).

Chemical control workloads on localized weed infestations typically fall from approximately 4 worker-days/species during the first year, to 2.5 the second, 2 the third, and 1.25 subsequently (Tunison & Zimmer, in press). Locating and recording the plants during the first year accounted for the high initial time involvement. Time has to be spent in subsequent years monitoring the results of control until eradication can be demonstrated. Success has been achieved with only one plant to date, *Benicasa hispida*. Several other species are on the verge of eradication. Occasional introductions from adjacent areas outside the park will require continuous monitoring for some and eradication program for others.

BIOLOGICAL CONTROL

In some ways biological control is the neatest way of handling alien plant invasions. Once effective control agents are introduced the solution is long-term. However, the necessary research is expensive, implementation may take up to 10 years, success is not guaranteed (to date only about 50% of the attempts have worked), there are ecological risks, and political factors can supersede

scientific study (Markin, 1989). All of these negative factors notwithstanding, 43 insects and one fungus have become established on 21 weed species in Hawaii (Funasaki et al., 1988). Eight species have been very effectively controlled, three partially controlled, and 10 unaffected. Greater success might have been achieved if post-release studies had been conducted with further releases where and when necessary.

The control of forest and natural area pests has not been a high priority in Hawaii; rather, attention has been directed at agricultural species. However, the need for a forest pest biological control program was discussed by interested individuals in several government agencies as forest problems continuously failed to rise in priority above significant agricultural pests. It began as managers in Hawaii Volcanoes National Park became increasingly alarmed at the spread of *Passiflora mollissima*. Initially, it was thought that, by the park putting up some exploratory money, the state legislature would support a state program. The park also offered to convert an old greenhouse into a quarantine facility. Seventy thousand dollars of NPS money was guaranteed to carry out the conversion. The conversion actually cost about $150,000 on completion. However, we had still not established a recognized program. The conversion money was contingent on forming an operational interagency agreement. This objective was pursued quite aggressively and initiated the organization of a cooperative biological control research effort among the following agencies, each with specific responsibilities:

—National Park Service: sponsor plant pathologist and an insect quarantine station in Hawaii Volcanoes National Park.

—U.S. Forest Service: sponsor biocontrol entomologist and associated staff.

—State of Hawaii Department of Land and Natural Resources, Division of Forestry and Wildlife: provide program leadership and subsidize most foreign exploratory work.

—State of Hawaii Department of Agriculture: facilitate government relations and oversee regulation.

—University of Hawaii at Manoa: provide post-release studies and evaluation.

The interagency program has worked well with a number of organisms about to be released to control *Clidemia hirta* and *Passiflora mollissima*. Research is continuing on these species as well as *Myrica faya, Rubus argutus,* and *Ulex europaeus*.

Biological control has had a long history in Hawaii. There have been some very injudicious introductions, e.g., mongoose (*Herpestes auropunctatus*), carnivorous snail (*Euglandina roseus*), giant toad (*Bufo marinus*), but most of them were made before biological control had developed as a science (Funasaki et al., 1988). However, Howarth (1985) has summarized the potential limitations and drawbacks of biological control, having previously expressed considerable opposition to the program in Hawaii (Howarth, 1983). Funasaki et al. (1988), in a comprehensive review of biological control introductions in Hawaii, pointed out that "no purposely introduced species, approved for release in the past 21 years, has been recorded to attack any native or other desirable species."

The only effective mechanism available to managers to control widely distributed weeds is biological control. Unfortunately, some species are not amenable to this technique because of political constraints, e.g., the target species is grown as an ornamental (gingers) or crop (guavas) or is related to one. The sugar industry will resist any attempt to bring in biological control agents against grasses because of the remote possibility that they could slip over to sugar cane. The rapid decline of the industry in Hawaii may remove this hurdle. Meanwhile, managers will have to control such weeds in special areas using other techniques.

MONITORING

A monitoring program is essential for successful resource management. Yet it is the one part of a program that managers will frequently ignore because the utility of monitoring is not understood.

However, a good monitoring program provides a realistic measure of the effectiveness of the control program, gives early information when a control program is inadequate, and is a powerful tool in public relations and for justifying increased support.

Discussion

All weed control programs are expensive and have their drawbacks. Compromises have to involve expediency, politics, the resource being conserved, and other factors. Thorough documentation and detailed analysis of the prospects for satisfactory completion of a management program help validate programs. It also helps to have some of the key policymakers visit the area for field orientation. The demonstration of the effectiveness of a pilot program can be extremely persuasive. The complexity or difficulty of a management program should never be minimized. Administrators need to understand the issues.

Managers must take a more aggressive stance in the enforcement of importation controls. However, there are problems where there is a significant tourist industry. In Hawaii, the inspection of incoming passengers' baggage would meet with vigorous opposition. Apart from the expense, the potential inconvenience or antagonism of arriving passengers would kill the proposal. Government is extremely reluctant to do anything that might impact the state's primary industry. However, it is the returning or potential residents who are probably the greatest offenders as they try to smuggle in pets or potentially lucrative horticultural items. First-class mail is another avenue of introduction because it is not inspected. Even so, these may not be the significant modes of introduction. Beardsley (1979) has recorded the introduction of a number of insect pests through the years, many of which are attributable to uninspected military shipments. For example, the recent record of two brown tree snakes in Hawaii were imported via military shipments from Guam, where the snake has almost extirpated the native avifauna (Fritts, 1987).

Education is an important defense against unwanted introductions. A program explaining the objectives of the park, the ways in which species are imported, and the need for cooperation can be developed tastefully. However, getting the message prepared, much less delivered in the right place at the right time, is much more difficult. Where the majority of traffic comes in by air they could be entertained by a short orientation movie. State authorities have been encouraged to develop such a program.

An area where researchers and their students can assist managers is the documentation of alien species. There is a natural tendency for researchers to look only at the native elements when working in such exotic areas as Hawaii and the Galápagos. They are unlikely to make herbarium specimens of weeds. However, researchers should be required to take notes on the distribution of selected alien species when working in a park. It would be best if they reported their observations and maps in a newsletter specific to the area, particularly if the information does not merit more formal publication. In this way, results that might be lost or discarded from files can be retrieved and are available to other people for comment and verification. Previous researchers should also be asked to make their field notes available to managers wanting to document alien species. An alternative strategy would be to ask researchers to document the presence or absence of a list of species in particular areas of concern. It is only by amassing databases of this nature that managers can get an understanding of rates of spread, impact, and population estimates of the species of concern. The added advantage is that managers can sometimes see a problem developing and take appropriate action before it becomes a major management program.

Considerable further research on the invasiveness of species is needed. Mack (1985) has suggested that current lists of weedy characteristics do not contain all traits common to invasive species. He advocated pairwise comparisons of the ecology of congeneric species, one member of the pair a weed, the other not a weed. He suggested that such a study would provide a better understanding of important determinants of weediness in given conditions. Less than 20% of the

plants introduced to Hawaii have become established in the wild, and only approximately 10% of those have become serious pests. Experience shows that certain families and types of plants must be prohibited from the islands (Smith, 1985), e.g., early successional and gap replacement species and members of the Melastomataceae, Myrtaceae, Passifloraceae, and Poaceae. Weeds known to be noxious elsewhere should also be excluded. It is very hard to understand why *Clidemia hirta* was introduced to Hawaii after its known behavior in Fiji. However, it is thought that the forester Lyon brought it in as a potential ground cover for eroded watershed areas.

Alien plant control is possible even in overwhelming situations. Successful programs depend on a thorough understanding of the biology of a weed and its history in the ecosystem. High-level administrators need to participate in early planning. Field excursions where administrators can see problems and discuss the management program are important. Managers should be as realistic about the cost of a program as possible. Projects should never be underestimated as a means of obtaining administrative approval. Administrators nearly always want to prune budgets. A manager who has developed a defensible lean program is far more likely to succeed than one who under- or overestimates. Also, educating visitors on the intent and needs of a management program is time well spent. When the public understands and supports a program's objectives, administrative support is forthcoming.

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THE ROLE OF HERBICIDES IN MANAGING CONSERVATION LANDS[1]

Philip S. Motooka[2]

Abstract

Pesticides suffer an exaggerated reputation for health and environmental hazards. Herbicides in particular are very safe, much safer than mechanical and manual means of weed control. Moreover, herbicidal weed control is usually more effective and economical than mechanical means. The adverse effect of herbicides is nil with proper management. The choice of herbicides, appropriate methods of application, and timely application will ensure no hazard to applicators, indigenous flora, or ground water. Furthermore, the nature of the problem of weed management in conservation areas mitigates environmental effects of herbicides. Typically, the area that requires treatment is small, and applications are required infrequently, so the amount of herbicide introduced into the ecosystem is minute. They have no impact on the environment, except for target plants, and they are rapidly neutralized by degradation. With proper techniques, herbicides can be applied foliarly to weeds without hazard to nearby plants, and there are other, target-specific ways to apply herbicides: the basal bark, cut-surface, and cut-stump methods. Much work has been done in Hawaii on the chemical control of tropical weed species. A summary of results is presented. To achieve judicious herbicide management, research must establish the efficacy of candidate herbicides and methods of application for each species and circumstance, and applicators must be trained to avoid waste, non-target plant injury, contamination of the environment, and health risks.

Biologists often overestimate the hazard of pesticides to human health and the environment (Smith, 1984; Weis, 1986). As a result, there is a reluctance to utilize herbicides to control alien plants in natural ecosystems. The United States National Park Service, for example, forbids the use of 2,4-D (2,4 dichlorophenoxy acetic acid), despite the fact that experts consider 2,4-D safe and that it is readily available in supermarkets as a lawn herbicide.

Manual and mechanized means of plant control are frequently and erroneously thought to be safer to workers and the environment than herbicidal plant control. However, there is a preponderance of evidence that pesticides and especially herbicides, properly managed, are not a significant health or environmental threat (Coun. Agric. Sci. Tech., 1985; Walstad & Dost, 1984; Whelan et al., 1983). Sharp implements and power equipment make farming the hazardous profession that it is (Orr & Leng, 1981). Moreover, mechanical methods of plant control are likely to disrupt the soil and expose it to erosion (Beasley et al., 1986; Coun. Agric. Sci. Tech., 1982) and reinvasion (Anderson, 1983).

Herbicides are usually more economical and effective than mechanical weed control. Grubbing, for example, is labor-intensive and ineffective for species capable of sprouting from root fragments and rhizomes left behind. Herbicides with preemergence activity can control weeds germinating from seed for weeks or months after treatment.

Many people fear pesticides regardless of their toxicity, dose, persistence, mobility in the environment, and bioaccumulation potential. All of these factors are critical to establishing the potential hazard to humans and the environment. Proper management of pesticides with due consideration of pesticide properties and environmental factors would preclude such problems. Because herbicides

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are not subject to bioaccumulation and tend not to be highly toxic, they pose less of an environmental threat than other classes of pesticides.

The circumstance of the natural ecosystem mitigates the impact of herbicides upon it. Application of herbicides in natural ecosystems would be confined to relatively small areas or even to individual plants. Typically, applications would be required infrequently compared with cropland. Hence the amount of herbicide released into the natural ecosystem would be relatively minute.

Nevertheless, herbicides must be managed judiciously to prevent contamination and unintended environmental impact and also to achieve efficacy and economy of weed control.

Application Methods

The several methods of applying herbicides vary as to efficacy, economy, and potential environmental impact.

To achieve maximum benefit and economy with minimal environmental impact, herbicide applications must be precise in rate and placement, and the method of application must be appropriate for the species and situation.

FOLIAR SPRAY

Foliar spray application is an easy and labor-efficient method of applying herbicides. With proper applicator training and equipment calibration, the applicator can apply herbicides precisely. Except in cases of very close proximity of non-target species to target species, directed or spot applications can be made without danger to the non-target species.

The optimal spray application requires many fine droplets uniformly distributed over the weed canopy (Behrens, 1957; McKinlay et al., 1972). The weed should be reasonably vigorous and translocating basipetally. Too high an herbicide dose will interrupt translocation and result in less herbicide being translocated out of the leaves (Hay & Thimann, 1956; Leonard & Crafts, 1956).

Woody plant control usually requires repeat applications, particularly in humid tropical areas where climatic conditions augment the tolerance of plants to herbicides (Motooka, 1986). Such repeat applications need to be made at intervals of 9–24 months, which should pose no hazard to the ecosystem.

Similarly, regrowth flushes after drought or mechanical clearing can be set back by follow-up with herbicides (Amor, 1975; Amor & Richardson, 1980; Cates, 1967; Eaton et al., 1970; Ghosh, 1980; Ivens, 1971, 1979; Johnson & Back, 1977a, b; Meeklah & Mitchell, 1981; Upchurch et al., 1969). Immediately after rapid flushes of growth, the energy reserves of the plants are low, the leaves are succulent and therefore readily penetrable by herbicides, basipetal translocation is active, and the weed biomass is small.

Drift prevention measures—attention to wind, use of low-pressure and coarse sprays, nozzles held low, use of nonvolatile formulations, and the use of hooded nozzles—will preclude injury to non-target plants.

A good deal of work with foliar applications has been conducted in Hawaii on *Psidium guajava* L. and *Lantana camara* L., weeds that have long been problems there (Motooka et al., 1969) as well as in the Galápagos. *Psidium guajava* is one of the few woody plant species that is susceptible to 2,4-D (Motooka, 1981). Applications of 2 kg/ha repeated once or twice over 18–24 months have resulted in virtually complete kill in tests (Hawaii Instit. Trop. Agric. Human Resour., 1984) and under actual usage. Dicamba (3,6-dichloro-*o*-anisic acid) and picloram (4-amino-3,5,6-trichloropicolinic acid) were also effective (Hawaii Instit. Trop. Agric. Human Resour., 1982).

Lantana camara was tolerant of 2,4-D, 2,4,5-T (2,4,5-trichlorophenoxy acetic acid), and dicamba. Picloram was effective at 1 kg/ha (1/2% v/v spray) (Hawaii Instit. Trop. Agric. Human Resour., 1982, 1984).

FOLIAR—WIPE-ON

Wipe-on methods, which employ absorbant rope (rope-wick) (Dale, 1978) or other materials soaked with herbicide to wipe the herbicide directly onto the foliage of target plants, provide several advantages in weed control on conservation lands:

1. There is no drift.
2. Nonselective herbicides can be used since they are applied selectively.
3. Very little water is needed, an important benefit in remote areas without convenient water sources.
4. Very little excess herbicide is applied.
5. Small, hand-held units would be easily portable in rough, remote terrain.

On the other hand, there are disadvantages to wipe-on methods:

1. The herbicide is not uniformly distributed over the target plant, although this is partially rectified by wiping on in two opposite directions.
2. There must be a height differential between the weed and the desirable plants.

Obviously, wipe-on applicators are not practical against rigid woody plants. However, they are useful against young saplings, forbs, and grasses.

Both 2,4-D and dicamba wiped on to *P. guajava* saplings gave adequate control (Hawaii Instit Trop. Agric. Human Resour., 1985). However, as with spraying, repeat treatments would be required for a kill. Wipe-on treatments were also effective on *Solanum sodomeum* L. (Hawaii Instit. Trop. Agric. Human Resour., 1985) using dicamba and picloram, on *Verbena littorallis* HBK using 2,4-D, and on grasses using glyphosate (N-(phosphono-methyl) glycine) (unpublished data).

FOLIAR—UYEDA DRIZZLE APPLICATION

The Uyeda Drizzle Application (UDA) method was developed by Shigeo Uyeda of the McBryde Sugar Company, Eleele, Hawaii (Motooka et al., 1983). Any conventional sprayer, including knapsacks, can be converted to a UDA unit by replacing the nozzle with an orifice disc having an orifice 0.35–0.51 mm in diameter. The strainer should be 100 or 200 mesh, and the wand should be straight.

Rather than an atomized spray, the UDA unit expels a fine stream. When the wand is waved more or less horizontally the herbicide is broadcast over a swath width of up to 10 m, depending on the angle of the swing. By aiming the wand, a very precise spot application is achieved; the application can selectively kill grasses in sugar cane rows with glyphosate (Shigeo Uyeda, 1983, pers. comm.).

The UDA method is a low-volume method, a volume rate of 13 l/ha is usually adequate.

The advantages of the UDA method to the conservation-land manager are:

1. Little drift potential
2. Low water requirement
3. Simple and low-cost parts to convert a conventional sprayer to a UDA unit
4. Versatility, easy conversion back to a conventional sprayer
5. A "reach" of 5 m horizontally or vertically on brambles and tall weeds without significant drift

The disadvantages are:

1. Herbicide distribution consisting of large, sparsely distributed droplets
2. Requirement for clean water to prevent clogging of the orifice
3. Restriction to liquid herbicides

TABLE 1. Susceptibilities of some woody species to herbicides applied by notching. References from Hawaii Instit. Trop. Agric. Human Resour.

Species	Herbicides
Acacia confusa Merr.	2,4-D, dicamba, glyphosate, picloram (HITAHR, 1985)
Acacia decurrens var. *dealbata* (Link) F. Muell.	Dicamba, glyphosate, picloram (HITAHR, 1985)
Casurina equisetifolia L.	Dicamba, glyphosate, picloram (HITAHR, 1985)
Fraxinus uhdei (Wenzig) Lingelsheim	2,4-D, dicamba, glyphosate, picloram (HITAHR, 1986)
Grevillea robusta A. Cunn.	Dicamba, glyphosate, picloram (HITAHR, 1985)
Manihot glaziovii Muell-Arg.	Picloram (HITAHR, 1983)
Schinus terebinthifolius Raddi	Dicamba, glyphosate, picloram, 2,4,5-T (HITAHR, 1982, 1983)

UDA applications of 2,4-D have suppressed *P. guajava* for one year (Hawaii Instit. Trop. Agric. Human Resour., 1982). UDA-applied picloram was effective on *L. camara* (Hawaii Instit. Trop. Agric. Human Resour., 1984). The method has been well accepted by a few ranchers and conservation-land managers in Hawaii for control of *Brachiaria mutica* (Forsk.) Stapf and other grasses with glyphosate, of *Schinus terebinthifolius* Raddi and *Caesalpinia sepiaria* Roxb. with picloram, and of *Triumfetta bartramia* L. with picloram and dicamba.

BASAL TREATMENTS

Large shrubs and trees are often difficult or impossible to spray without hazard to nearby desirable plants. Where foliar sprays are not appropriate, basal treatments are preferable.

Basal treatments are usually more effective than foliar sprays and, since the targets are treated individually, are extremely target specific. However, the labor requirements and risk of injury to personnel are much higher for basal treatments.

BASAL TREATMENTS—CUT-SURFACE

Cut-surface treatments involve the application of herbicides directly into the xylem (Klingman & Ashton, 1975; Motooka et al., 1982). Although there are tree injectors to do this, this can also be accomplished by hacking notches in the trunk with a machete or ax, and brushing or squirting 1 ml of herbicide into each notch. Depending on the tolerance of the target species to the herbicide, notches are made at intervals or end-to-end in a continuous ring around the trunk.

With notching, *P. guajava* was readily controlled with 2,4-D. Dicamba and picloram were also effective (Hawaii Instit. Trop. Agric. Human Resour., 1982, 1983, 1984). *Psidium cattleianum* Sabine was sensitive to the same herbicides (Hawaii Instit. Trop. Agric. Human Resour., 1985, 1986).

Susceptibilities of some other Hawaiian woody weed species to herbicides applied by notching are presented in Table 1.

Australian workers (Anderson, 1974; Robertson, 1974, 1979; Robertson & Moore, 1972; Robertson & Young, 1976) controlled several species of eucalypts by cut-surface treatments using picloram plus 2,4-D or picloram plus 2,4,5-T.

Larger trees may require greater doses of herbicides than can be applied to notches, which are rather shallow (2–3 cm). For such trees, holes can be drilled into the trunk. *Eugenia jambos* L. was thereby killed by application of picloram, glyphosate, and 2,4,5-T (Hawaii Instit. Trop. Agric. Human Resour., 1984). *Persea americana* Micc. was controlled with glyphosate (Hawaii Instit. Trop. Agric. Human Resour., 1986), which was the only herbicide tested.

BASAL TREATMENTS—BASAL BARK

The basal bark method requires an oil-soluble herbicide formulation, such as an emulsifiable concentrate. The herbicide is diluted to 4%–8% v/v in an oil, for instance, diesel fuel. This solution is applied completely around the base of the trunk from ground level to approximately 30 cm. Enough of the solution is applied to cause wetting of the bud zone of the root crown by runoff from the trunk (Klingman & Ashton, 1975; Motooka et al., 1982). The greatest advantage of this method is that the labor and hazard of notching the trunk is eliminated.

In Australia, basal bark treatments with 2,4,5-T or with 2,4,5-T plus picloram-controlled eucalypts (Robertson, 1979; Robertson & Pedersen, 1973). Adding picloram to the mixture enhanced control and reduced the variability of response (Robertson & Pedersen, 1973).

Psidium guajava and *Melastoma malabathricum* L. are readily controlled by the basal bark method using a 4% v/v solution of 2,4-D or 2,4,5-T in diesel (Hawaii Instit. Trop. Agric. Human Resour., 1984). Based on the efficacy of foliar-applied 2,4,5-T, this herbicide would probably be effective on several other species. However, cancellation of all registrations of 2,4,5-T in the United States has ended research with it. Trichlopyr, available in a lipophilic formulation, may expand the spectrum of susceptible species to basal bark treatments.

BASAL TREATMENTS—STUMPS

When there is a need to remove the aerial parts of woody plants immediately, the remaining stumps can be killed by applying herbicides to them.

For cut-surface treatments, it is imperative that the herbicide be applied immediately after cutting. Even a five-minute delay may be too late as this allows air into the xylem, effectively locking out the herbicide. This treatment is more effective during drought periods when the sap is under higher tension and can draw the applied herbicide deeper into the stump (Hay, 1956).

Psidium guajava stumps are readily killed by cut-stump treatments with 2,4-D in drought though not in the rainy season (Hawaii Instit. Trop. Agric. Human Resour., 1984). *Melastoma malabathricum* stumps were killed with dicamba, picloram, and 2,4,5-T; 2,4-D caused severe injury; and glyphosate was ineffective, all in a high-rainfall area (Hawaii Instit. Trop. Agric. Human Resour., 1984).

In Australia, Anderson (1974) and Robertson (1979) reported that cut-stump treatments of eucalypts with 2,4,5-T, 2,4-D plus picloram, and 2,4,5-T plus picloram were each effective.

An alternative stump treatment is application of the oil-herbicide solution used in basal bark treatments. This alternative does not require treatment immediately after cutting and may be more effective after some regrowth when the energy reserves of the plant have been exploited to fuel the regrowth. Also, the stumps are easier to see after they have resprouted. *Melastoma malabathricum* stumps were killed by treatment with 2,4-D and with 2,4,5-T in diesel (4% v/v) (Hawaii Instit. Trop. Agric. Human Resour., 1984).

Conclusion

In addition to the variety of herbicides available to the conservation-lands management, options in methods of application greatly expand the utility of herbicides for controlling alien plants. With research and proper staff training, the manager can suppress alien plants with safety, efficacy, and economy that cannot be matched by mechanical methods.

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CONSERVACION Y MANEJO DE LA VEGETACION EN GALAPAGOS

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RESUMEN

Los problemas de manejo y protección de la vegetación nativa de las islas Galápagos no han sido evaluados suficientemente. Las condiciones particulares de cada isla y la influencia de diversas especies y asociaciones de plantas introducidas requieren de análisis separados para definir estrategias adecuadas a cada caso. La erradicación total de plantas introducidas será posible solo en algunos casos, mientras que en otros unicamente se podrá controlar su diseminación. Las acciones de control y erradicación llevadas a cabo hasta ahora han enfocado una parte muy pequeña del problema, tanto en alcance como geográficamente. Considerando que las islas pobladas: Santa Cruz, San Cristóbal, Floreana e Isabela son las de más alta prioridad por presentar la situación más crítica, las acciones de manejo deben considerar las necesidades de las poblaciones humanas residentes, para buscar una solución integrada y real al problema de conservación de la vegetacion nativa. El uso de plantas nativas y de plantas introducidas que han demostrado ser inofensivas, para reforestacion y otros propósitos (cercas vivas, forraje, sombra y fijación de nitrógeno) podría ser un mecanismo para lograr la participación pública que se necesita para garantizar la permanencia de los recursos florísticos de las islas Galápagos.

Las soluciones a los problemas generales de conservación en las Islas Galápagos no pueden esperarse de una sola persona o sector. Necesariamente deben ser planteadas desde un punto de vista integrado y por ello compete a un grupo de personas e instituciones el compartir esa responsabilidad.

En lo que se refiere exclusivamente a las plantas, el problema debe ser analizado tomando en cuenta varias facetas.

En primer lugar, debe reconocerse que ha existido un gran desequilibrio de interés y atención para los animales y las plantas de Galápagos. Los exitosos y reconocidos esfuerzos que se han hecho para proteger la fauna de las islas no son comparables a los recientes e incipientes esfuerzos realizados con las plantas. Aunque dentro del sistema las plantas están protegidas, los problemas específicos que afectan a la vegetación, aunque serios, no han recibido la atención apropiada, debido a los siguientes factores principales:

1. Los estudios e investigaciones se han realizado con una fuerte orientación autoecológica y taxonómica, con mucho menos esfuerzo e interés por estudiar la estructura y dinámica de la vegetación y de las comunidades representativas. Esta situación, sin ser mala, no ayuda mucho a las decisiones de manejo que requieren más bien de conocimientos del conjunto y de su funcionamiento, más que de los elementos que lo forman considerados por separado.
2. Hasta ahora, ha faltado una apreciación y evaluación general del problema en todo el Archipiélago considerando, por supuesto, las circunstancias particulares que afectan a cada isla. Solo en base a esa evaluación se podría conocer la magnitud real del problema, clasificar los factores que lo determinan, identificar situaciones o áreas críticas, y establecer prioridades.
3. Por lo dicho en el número dos, las acciones de manejo que se han realizado hasta ahora han estado dirigidas a la solución de problemas específicos y muy localizados; especialmente tratando de combatir la diseminación de ciertas plantas introducidas muy conspicuas.

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4. La falta de valoración de las necesidades humanas básicas que son satisfechas con el uso de productos de especies nativas es otro de los factores determinantes de la situación actual. Las poblaciones humanas del Archipiélago están obligadas a usar los productos, bienes, y servicios del Parque porque no existe otra opción. Este es, probablemente, el punto más delicado en el tratamiento del problema, dadas sus implicaciones pasadas, presentes, y futuras. Cualquier solución que trata de enfocar el asunto ignorando la demanda y necesidades de las poblaciones humanas existentes en las islas, no tendría esperanza de éxito o constituiría una respuesta temporal. Si el uso de los recursos y productos vegetales nativos es un problema para la protección de los sistemas naturales, hay que reconocerlo, entenderlo, y dirigirlo de manera tal que los impactos sean los menores posibles.

5. Sumando a todo lo anterior está la crónica escasez de recursos, tanto del Servicio del Parque Nacional Galápagos como de la Estación Charles Darwin. Especialmente el primero requiere de personal, equipo, y materiales suficientes para ejecutar las labores de campo.

Se han hecho algunos esfuerzos y se han realizado campañas y ensayos de erradicación en la parte alta de Santa Cruz, sobre todo en el área de Media Luna, combatiendo la guayaba (*Psidium guajava*) y la cascarilla (*Cinchona succirubra*). También se han erradicado manualmente las plantas introducidas a lo largo de la carretera Puerto Ayora–Canal de Itabaca. Sin embargo, los éxitos son relativos y los ensayos continúan con un grupo de guardaparques que nunca ha podido ser de más de 10 personas. Por esa misma limitación de recursos, los esfuerzos se han centrado en Santa Cruz, a donde, sólo en 1983, fueron introducidos alrededor de 50 nuevos taxa de plantas.

Los problemas en las otras islas ni siquiera se han evaluado y las acciones directas de control y/o erradicación han sido nulas. Sin embargo, la cobertura de las plantas introducidas aumenta en forma obvia y nuevas especies aparecen como más agresivas que las anteriores.

El problema de la conservación y el manejo de las plantas en Galápagos, debe enfocarse desde dos ángulos principales:

a. Las plantas introducidas y sus consecuencias.
b. El uso de las plantas nativas por parte de las poblaciones humanas.

La situación de las plantas introducidas difiere de una isla a otra, en número de especies, en especies dominantes, en extensión de las áreas afectadas, en "edad" de los problemas presentes, y en la relación entre animales y plantas introducidas en términos de clareo y diseminación.

Cada isla requiere de un análisis y evaluación por aparte, tomando en cuenta que el mayor peligro existe en las islas habitadas, aunque algunos casos de islas deshabitadas, como San Salvador, son también críticos.

Considerando el problemo de manera general, la más alta prioridad para las acciones son las cuatro islas pobladas: Santa Cruz, San Cristóbal, Floreana, e Isabela. En estas islas reside una población de aproximadamente 10,000 personas que viven tanto en los puertos como en las fincas ubicadas en las zonas altas y húmedas. Especialmente en este último caso, dados los sistemas de producción agropecuaria, la influencia directa o indirecta sobre la vegetación nativa ha sido determinante, desde que se inició la colonizacion de las islas en 1832.

Ligado a esta situación, en cada isla debe considerarse también el grado de influencia como agentes diseminadores que ejercen las poblaciones de animales introducidos. La mayor o menor atención al manejo de ganado doméstico es otro de los factores que debe considerarse entre los más críticos.

Sin ninguna duda Santa Cruz y San Cristóbal son las dos islas mayormente expuestas a nuevas introducciones de plantas, por centrarse en ellas las actividades económicas del Archipiélago.

Dada la extensión y complejidad del problema de las plantas introducidas en cada una de las islas, no es posible vislumbrar una solución fácil ni a corto plazo. Mientras en unos sitios podría ser posible la erradicación total, en otros lo único factible parece ser el control de la diseminación.

FIGURA 1. Un ambicioso programa de reforestación se ha iniciado en isla San Cristóbal usando plantas nativas como *Scalesia pedunculata*. Además de asegurar la supervivencia de especies nativas, se trata de proteger las fuentes de agua de las cuales depende la población humana. (Foto por O. Hamann.)

No hay duda de que las técnicas manuales de control y erradicación no serán suficientes para enfrentar la situación, ni siquiera contra una sola especie. Durante los últimos 15 años, cada técnica probada ha dado resultados parciales, y es lógico suponer que una aplicación sistemática y secuencial de diferentes métodos y técnicas podrían sumar resultados hasta lograr el éxito buscado.

Sin embargo, todo esfuerzo será inútil si no se desarrolla una campaña de educación que alcance a todos los niveles de la población. Ningún sistema de control será efectivo, aunque exista suficiente personal de vigilancia, si no se logra una "consciencia pública" que produzca un autocontrol.

El uso de ciertas especies nativas para obtener leña, madera para construcción, postes, estacas para cercas, y otras cosas; complica mucho más la situación de las comunidades naturales ya presionadas por la presencia de plantas exóticas.

Para satisfacer la demanda de productos vegetales se ha mencionado siempre la necesidad de proporcionar sustitutos para las especies nativas explotadas, usando especies introducidas adaptadas.

Durante los últimos años se han iniciado experimentos usando no sólo especies introducidas ya presentes en las islas, sino también las mismas especies nativas que están siendo explotadas, pero manejadas con técnicas silviculturales dentro de las fincas y en bosquetes de producción (Figs. 1, 2).

La posibilidad de utilizar especies introducidas presentes en las islas desde hace muchos años como plantas de uso múltiple podría disminuir la necesidad de nuevas introducciones. Tal es el caso de las leguminosas arbóreas como *Erythrina poeppigiana* que sólo recientemente han empezado a usarse en experimentos para cercas vivas, sombra de potreros, forraje adicional, y fijación de nitrógeno.

FIGURA 2. También algunas especies inofensivas de árboles introducidos como *Juglans neotropica* están siendo usadas en el programa de reforestación de San Cristóbal. (Foto por O. Hamann.)

Tectona grandis, que ha estado en Santa Cruz por más de 40 años, no se reproduce por semillas. Los experimentos de reproducción vegetativa permiten asegurar que podría ser una buena opción para producir madera de calidad.

Por ser las plantas el nivel primario del sistema, por tratarse de un archipiélago aislado, y por existir expectativas socioeconómicas, la solución a los problemas de las comunidades vegetales de Galápagos pueden ser dadas sólo a través de un manejo integrado de recursos.

Las soluciones parciales en extensión y alcance no son soluciones, las recomendaciones que respondan a intereses específicos difícilmente podrán integrarse, las acciones en sitios pequeños y específicos que tratan de proteger aspectos muy particulares llevan sólo a crear ''islas'' dentro de islas y no son significativas frente al problema en general.

Las soluciones serán viables en la medida en que los problemas se analicen en su dimensión real, no sólo de los límites del Parque Nacional hacia adentro, sino considerando que la satisfacción de las necesidades básicas de las poblaciones humanas de las islas es la única garantía para que permanezcan los sistemas naturales que se desea proteger.

THE COLONIZATION OF SAN CRISTOBAL, GALAPAGOS ISLANDS—A HISTORICAL PERSPECTIVE

Jacinto Gordillo[1]

Abstract

The history of human colonization of San Cristóbal, Galápagos Islands, is briefly summarized. Many alien plants have been introduced with humans, and some of these have changed the natural ecosystems considerably. The most aggressive alien plant species are identified, and recommendations are made for minimizing their impact.

San Cristóbal is the easternmost island in the Galápagos Archipelago and contains some unique biotopes, such as the famous El Junco crater lake, and the creeks La Toma, La Honda, and La Policia. Different vegetation types and plant communities that are rare in Galápagos can be found, such as bogs and fens (Itow & Weber, 1974). A number of plant species are endemic to this island, including *Scalesia incisa*, *S. divisa*, and *S. gordilloi*, the last-mentioned recently described from the southern coast of the island (Hamann & Wium-Andersen, 1986). *Scalesia pedunculata* also occurs on San Cristóbal, where it used to be a dominant species in the evergreen forest. Other rare plants restricted to this island worth mention are *Lecocarpus darwinii* (Adsersen, 1980) and *Calandrinia galapagosa*. Without doubt, San Cristóbal is very interesting biologically, but it has never been explored fully, because it generally is regarded as the island in the archipelago most altered by human settlement. Indeed, in connection with the colonization of the island, large areas were modified or completely cleared of their original vegetation to make place for crops. During the early colonization, most of the land suited for agriculture was transformed into fields of sugarcane, market gardens, and orchards. Nevertheless, large areas in the northern, more arid part of San Cristóbal and the valleys of the highland still remain in good shape, worthy of further investigations and conservation efforts.

The Colonization

Hickman (1985) recently described the colonization of the Galápagos Archipelago. In San Cristóbal, the first settlers to arrive were Manuel J. Cobos and José Monroy in 1866, when they formed a company to exploit the lichen known as "orchilla moss" (*Rochella babingtonii*), which is common in most of the islands. However, this venture failed and Cobos started to build up a settlement based on cultivated crops. Around 1869 Cobos established a new farm and settlement, called El Progreso, with 10 workers. He introduced many cultivated plants, such as sugarcane, bananas, coffee, guava, papaya and other tropical fruits. In 1888, after a ten years' absence from the island, Cobos started growing sugarcane on a large scale, with the help of a group of about a hundred convicts. A sugar mill and a wharf were constructed, and large areas were planted with sugarcane. At one time Cobos reportedly had 220,000 plants of coffee and 60,000 of bananas, in addition to the large fields of cane, and the yields he obtained were good, so the group of workers was enlarged. In 1904, however, Cobos was killed by his workers, who rebelled against the atrocious treatment they received (see Hickman, 1985). At that time the settlement numbered some 250 workers, but following the death of Cobos they all left the island, at least temporarily. Despite

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this, the settlement continued, and by 1922 there were about 530 people in El Progreso (E. Maldonado, unpublished report). The Cobos farm was closed in 1930, but the local people continued to live there and increased slowly in number. In 1949, because of the earthquake in Ambato in continental Ecuador, a new group of settlers arrived on San Cristóbal increasing the population abruptly to 1,000.

The following year, a Franciscan mission was established. This led to increasing public and official interest from the mainland, and various agricultural and state institutions came to the island. The village of Puerto Baquerizo Moreno at the coast started to grow, and a large group of people arrived in 1960–1961, when the Loja province in the mainland suffered from severe droughts. Most of these people settled in Cerro Verde. Thus the settlements grew during quite a long period, and eventually the island became the administrative capital of the archipelago.

In 1973, the Galápagos Islands were declared a province, which resulted in many social and political changes. More people arrived to take up duties as employees in newly established government institutions, particularly in 1980, when INGALA (National Institute for Galápagos) was established. During the same period, the increasing flow of tourists to the Galápagos also had its effect on San Cristóbal and made the development of a better infrastructure necessary. A new landing strip and airport were opened in 1986, whereupon regular commercial flights from mainland Ecuador to San Cristóbal were initiated; the growing number of tourists also made the construction of new roads, hotels, and restaurants necessary. At present the population of San Cristóbal is around 3,000 persons; the development of infrastructure to serve the population and the tourism still lags.

Impact on the Natural Vegetation

When the cultivation at the Cobos farm ended in 1930, large areas, especially those with sugarcane, were left untended, so gradually they were invaded anew by native and alien plants. As it turned out, alien plants predominated in taking over these large formerly cultivated areas. The conditions were apparently very favorable for such species as *Psidium guajava, Eugenia jambos,* and *Furcraea cubensis,* because they were able to invade and establish themselves without serious competition from native plants. In other areas the continuing grazing by domestic animals cleared more land, and the animals spread the seeds of alien plants into otherwise undisturbed vegetation. Large areas in the highest part of the island were in this way converted from native forests to grasslands or guava thickets (van der Werff, 1979). Apparently the clearing of the highland of its forest cover also influenced the watershed balance negatively, because the water in the creeks diminished considerably during prolonged droughts, as in 1982–1983, which had not occurred before (Lawesson & Estupiñan, 1987).

The Most Aggressive Alien Plants

The common guava (*Psidium guajava*) was already recognized as an invasive alien by Maldonado (unpublished report) in 1922: "Among the fruit trees which have become acclimatised on San Cristóbal, should be mentioned the common guava, in yellow and red varities; it was planted close to the administration houses, from where it spread enormeously, so that it now is a very bad plague, forming inpenetrable thickets." Indeed, the guava forms large forests and thickets, probably occupying about 12,000 ha.

The poma rosa, *Eugenia jambos,* was probably introduced around 1949. Dense forests of this alien tree now occur between 200 and 400 m, and those forests are so dense that no other plant species is able to survive below the *Eugenia* trees.

Lantana camara has been introduced to San Cristóbal during the last ten years and has spread rapidly. It is now known from the coast to the upper part of the agricultural zone. It is feared that

FIGURE 1. *Rubus* from San Cristóbal, recently introduced to Galápagos but already covering large areas in the mesic highlands. (Photo taken by O. Hamann, 1987.)

this species will spread on this island as rapidly as on Floreana (Cruz et al., 1986; Lawesson & Ortiz, this volume).

An unidentified *Rubus* species should be mentioned, since it probably is one of the most aggressive alien plants hitherto introduced to Galápagos (Fig. 1). It was introduced to San Cristóbal no more than five years ago, probably by some farmer who wanted to collect and sell the delicious fruits. *Rubus* evidently has a very strong reproductive potential throughout the year, and it has been able to establish in the area around Cerro Verde, as well as in dry forest. From the original places of infestation it is now spreading to all the higher parts of the island and may well already cover as much as 100 ha.

RECOMMENDATIONS

The Galápagos National Park Service and the Ministry of Agriculture and Livestock should immediately develop and implement an eradication campaign against invasive alien plants on San Cristóbal, in particular *Rubus*. Considering that it will be impossible to eradicate fully, or perhaps even control, all alien plants, the long-term solution implies that the local inhabitants and visitors should be enlisted in a general and major campaign against invasive alien plants. As a necessary first step towards this, an information and awareness campaign should be mounted in the Galápagos to explain the severe adverse effects for farmland as well as for the National Park caused by invasive alien plants. Only in that way will it be possible to control such species and minimize the risk for new introductions.

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MANAGEMENT AND RESEARCH EFFORTS TO PROTECT VULNERABLE ENDEMIC PLANT SPECIES OF HALEAKALA NATIONAL PARK, MAUI, HAWAII[1]

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ABSTRACT

Assuming that the obvious threats of feral ungulates and alien plants to rare endemic flowering plants of Haleakala National Park are eliminated, what additional obstacles to survival of these plant species remain? The ecological status of selected endemic flowering plants of Haleakala is described to illustrate subtle problems relating to long-term survival. Better understanding of the ecology, life histories, and breeding systems of island plants as well as biological interrelationships among native and alien species—competition, allelopathy, mycorrhizal relationships, nitrogen fixation, pollination, dispersal, seed predation, and herbivory—is critical in conservation biology and management of island ecosystems.

Haleakala National Park, an 11,400-ha natural reserve that reaches from sea level to over 3,000 m elevation on the island of Maui, is generally recognized as one of the most intact natural areas in the Hawaiian Islands. Despite high natural biological diversity, its floristic and faunistic lists include about one-third introduced species (Table 1). Though not all these alien species have significant effects on native species and ecosystems, some have very serious effects. The effects of such alien species as pigs and goats are well documented, whereas effects of relatively inconspicuous alien vertebrates (e.g., rodents) and invertebrates may be devastating but are less documented. In response to a recent survey of national parks of the United States, the park staff produced a list of threats to the natural resources of Haleakala (Table 2). Current management at Haleakala emphasizes control of feral goats and pigs; these are regarded as the most serious threats to the park's biota. Control of selected introduced plants rates as an important secondary priority. Managers recognize that mitigating alien perturbations in vulnerable insular systems may require a costly sustained effort of research and management.

Our approach in this paper is to describe the ecological status of selected endemic flowering plant species of Haleakala National Park to illustrate the types of management problems encountered in the Hawaiian Islands, including subtle problems relating to long-term survival, and the role of pertinent research.

THE SILVERSWORD (*ARGYROXIPHIUM*) GROUP

The genus *Argyroxiphium* (Asteraceae) includes five species in the Hawaiian Islands, three of which, *A. sandwicense*, *A. grayanum*, and *A. virescens*, are native to Haleakala (Carr, 1985).

The Haleakala silversword (*Argyroxiphium sandwicense* subsp. *macrocephalum*) is a giant (to 2 m tall), monocarpic rosette plant (Fig. 1), endemic to the crater and upper slopes of Haleakala volcano at elevations of 2,000–3,000 m. It matures from seed to its flowering stage in a period that varies from as little as three years to many decades, depending on growth conditions. The plant remains a rosette until the final few months of its life, when it sends up a flowering stalk, sets seed,

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TABLE 1. Summary of the Haleakala's native and introduced biota. References: (1) Medeiros & Loope (unpublished), (2) Tomich (1986), (3) Conant & Kjargaard (1985). Endemism is evaluated for the Hawaiian archipelago.

Group	Numbers of native species	Numbers of introduced species	% introduced species	% of native species endemic	References
Flowering plants	257	310	55	90	(1)
Ferns and fern allies	103	5	5	63	(1)
Bryophytes	173	0	0	50	(1)
Mammals	1	9	90	100	(2)
Birds	15	17	53	73	(3)
Molluscs	34	9	21	100?	(1)
Insects	ca. 1,000	ca. 400	25–30	ca. 98	(1)
Total of above groups	ca. 1,570	ca. 750	ca. 32		

TABLE 2. Threats to Haleakala National Park in approximate order of decreasing severity as perceived by the park staff in February 1987, produced in response to a recent survey of "threats" to national parks of the United States.

1. Feral goat (*Capra hircus*)
2. Feral pig (*Sus scrofa*)
3. Strawberry guava (*Psidium cattleianum*)
4. *Clidemia hirta*, an alien plant (present on Maui but not yet in park)
5. Banana poka (*Passiflora mollissima*), an alien plant (present on Maui but not yet in park)
6. Argentine ant (*Iridomyrmex humilis*)
7. Alien western yellowjacket wasp (*Vespula pensylvanica*)
8. Fountain grass (*Pennisetum setaceum*) (present on Maui but not yet in park)
9. Alien plants (other than those listed above)
10. Alien mammal predators (mongoose—*Herpestes auropunctatus*, feral cat—*Felis domesticus*, feral dog—*Canis familiaris*)
11. Alien rodents (*Rattus rattus, Rattus exulans, Mus musculus*)
12. Avian disease and introduced birds
13. Alien parasites of native insects
14. Alien molluscs (especially *Euglandina rosea* and *Oxychilus alliarius*)
15. Alien long-legged ant (*Anoplolepis longipes*)
16. Aircraft noise from scenic tours (believed to be mostly an esthetic intrusion)

and dies. Flowering occurs June to September, with annual numbers of flowering plants varying in the past two decades from none to over 2,200. This spectacular plant gained fame in the early years of Hawaiian tourism. It had become so rare by the 1920s due to human vandalism and browsing by goats and cattle that it was believed near extinction. During the 1930s, after protection within the national park, much concern arose over the high level of seed predation by native insects, and proposals for destroying "infected" plants or for application of pesticides were considered but never applied. The Haleakala silversword has thrived and increased under protection and now numbers about 50,000 plants, mostly on cinder cones in Haleakala Crater (Kobayashi, 1973; Loope & Crivellone, 1986). Plots for study of its population dynamics suggest that many seedlings establish in some years, especially after heavy flowering, with few or no new seedlings appearing in other years. Substantial natural mortality may occur in some years due to erosion caused by heavy rains. Some seedlings are washed free of their loose cinder substrates, and others are buried by sliding cinder.

The silversword is pollinated by native bees, flies, and moths, attracted in large numbers to the

FIGURE 1. *Argyroxiphium sandwicense* subsp. *macrocephalum*.

giant, aromatic inflorescences. Carr et al. (1986) showed silverswords to be self-incompatible, requiring cross-pollination by insects for viable seed set.

The aggressive alien Argentine ant (*Iridomymex humilis*) became established in the park in the 1960s. It has occupied and is slowly spreading in comparable high-elevation habitat nearby on Haleakala's west slope at 2,100–2,800 m (Medeiros et al., 1986) and seems to present the only currently apparent serious threat to survival of silversword. The Hawaiian Islands lack endemic ants; hence the native arthropod biota is very poorly adapted to ant predation. Medeiros et al. found that the Argentine ant exerts a serious impact on the predominantly native arthropods, including

FIGURE 2. *Argyroxiphium grayanum.*

pollinators, in Haleakala's high-elevation ecosystem. In spite of the silversword's large population size, a loss of pollinators could result in a dramatic loss of seed set and subsequent collapse of natural populations.

The greensword, *Argyroxiphium grayanum* (Fig. 2), occurs at 1,600–2,100 m on northeast Haleakala and at 1,300–1,760 m on West Maui. Mean annual rainfall in its habitat is 5,000–10,000 mm. The greensword occurs primarily in bogs but occasionally occupies open, wet, montane ridgetops. In open bogs, the rosette grows with virtually no stem, directly on the ground like its alpine relative

the silversword. In dense rainforest, the greensword rosette grows on a polelike stem as much as 1.5 m in height. Some plants of this species grow unbranched for about 10–15 years in rosette form, then send up a large flowering stalk, set seed, and die. Others are multibranched, with up to 200 reduced rosettes, a condition caused by a native fly, *Neotephritis paludosae*, feeding on the apical meristems. The life histories of these multibranched plants and their role in reproduction remain unclear. Flowering phenology is similar to that of the silversword, with over a thousand greenswords blooming in some years and very few or none in others. Monopodial flowering plants reach 2 m or more in height.

Serious management problems for preservation of greenswords have arisen in the past few years. Feral pigs, released from low-elevation farms in recent decades, have established populations in the high-elevation rainforests of northeastern Haleakala (Diong, 1983). The greensword grows in bogs, small treeless areas scattered through the upper rainforest. In the search for food—probably alien earthworms and alien slugs (*Milax gagates* and other species) as well as native invertebrates—pigs have extensively rooted many of the bogs of the park. Direct damage by pigs to greensword plants has frequently been observed. Displacement of the seedlings from potential habitat by aggressive alien plants, especially *Holcus lanatus*, is another serious problem. These alien species will increase over time unless pigs are controlled in this remote area (Medeiros et al., in press). Bogs with minimal invasion of alien plant species when fenced have shown excellent recovery of endemic species including reestablishment of greensword seedlings. In four years of recovery from pig digging, cover of native vegetation in one severely damaged bog increased from 6% to 90% (Loope et al., in press).

Argyroxiphium virescens (Fig. 3) formerly occurred on the slopes of Haleakala in the lower shrubland zone (at ca. 2,000–2,500 m elevation) just above the upper limits of dense forest. This species was apparently not uncommon in the mid-1800s and was known from a number of disjunct populations in the park in 1910. It was last seen in 1945 and is presumed extinct. Extinction can probably be attributed to population reductions caused by the browsing of cattle and feral goats and subsequent reproduction problems of this probably self-incompatible species.

Lobelioids

The Hawaiian Lobelioideae (Lobeliaceae) may represent the greatest speciation from a single ancestral stock of any Hawaiian flowering plant (Rock, 1919; Wagner et al., in prep.). The endemic Hawaiian genera *Clermontia*, *Cyanea*, *Rollandia*, and *Delissia*, with at least 90 well-marked species, all evolved from a common ancestor. Many members of this group have undergone a precipitous decline, with dozens of species lost to extinction. Massive destruction of habitat by cattle and some extinctions were noted by the early Hawaiian naturalists Hillebrand (1888) and Rock (1919). Feral pigs and alien plant invasions have probably had the greatest negative effects on the lobelioids since the 1920s. Additional, poorly understood, factors may have played important roles. The nectars of numerous species of *Clermontia* and *Cyanea* have been determined to be primarily hexoses, the nectar-type associated with feeding by passerine birds (Lammers & Freeman, 1986). Endemic honeycreepers and honeyeaters (Drepanidinae, Meliphagidae) were almost certainly important in pollination of many plant species, including the native lobelioids. Most bird pollinators have been extirpated or their populations have been greatly reduced (Olson & James, 1984; Scott et al., 1986).

Haleakala National Park has about 20 species of *Clermontia* and *Cyanea*, primarily in rainforest habitats. The last individuals of *Clermontia haleakalensis*, a treelike species of the forest shrubland ecotone, were eliminated by cattle by 1919, only nine years after J. F. Rock discovered this last surviving population not far from the current park headquarters.

Clermontia tuberculata (Fig. 4) and *Clermontia samuelii*, although apparently never common, have survived into the 1980s in moderate numbers in their high-elevation rainforest habitat of

FIGURE 3. *Argyroxiphium virescens*.

FIGURE 4. *Clermontia tuberculata*.

northeast Haleakala at 1,500–2,000 m elevation. Feral pigs reached this habitat, only recently, so far in small numbers, and their elimination before their numbers increase is crucial for the two *Clermontia* species.

Cyanea haleakalensis is highly localized and survives in low numbers at an elevation of 900–1,100 m in rainforest of Haleakala's Kipahulu Valley. The plants grow on steep, rocky slopes, inaccessible to pigs and unaffected by the dense growth of the alien grass *Paspalum conjugatum* that covers most of the nearby forest understory.

Schiedea haleakalensis and *Plantago princeps*

Schiedea haleakalensis (Caryophyllaceae) and *Plantago princeps* (Plantaginaceae) represent species eliminated by feral goats except from perpendicular cliff faces. *Schiedea haleakalensis* is known from only a dozen specimens, all collected within the national park. Only two specimens of *Plantago princeps* (Fig. 5) are known in the park, although this species survives precariously on other islands. When goats are fully controlled within the park, these species will have an opportunity to partially recover, though seed set may prove a problem due to the extremely reduced population levels.

Santalum Haleakalae

Santalum haleakalae (Haleakala sandalwood, Santalaceae, Fig. 6) is a rare endemic found only at elevations of 1,800–2,625 m on Haleakala volcano. The species is a long-lived, hemiparasitic (Kuijt, 1969), small tree up to 5 m tall. Only 600–800 individuals survive. Flowering and fruit initiation occur continually throughout the year, and most fruits abort before reaching maturity. The few fruits that reach maturity are subject to rodent predation, primarily by *Rattus rattus*. Seedlings have been found only under two Haleakala sandalwood trees in Haleakala Crater in areas of very sparse vegetation. Trapping for rodents in these barren areas suggests extremely low rodent populations.

The purple fleshy fruits appear adapted for bird dispersal, but they are not known to be eaten by any surviving native or introduced bird. An extinct large Hawaiian bird may once have dispersed and possibly scarified sandalwood seeds. Passing through the digestive tract of introduced game birds aids germination of other hard-to-germinate native species.

Santalum haleakalae also reproduces vegetatively by root suckers in the absence of goat browsing; in spite of severe problems with reproduction by seed, its survival seems assured for the foreseeable future.

Pleomele auwahiensis

Only about 24 trees of this East Maui liliaceous endemic survive in the limited dryland forest of Haleakala National Park, but outside the national park it is still one of the most common trees at 600–1,200 m elevation on the rough lava flows of leeward Haleakala volcano, with many thousands of surviving individuals. This species must be considered endangered, since no reproduction is occurring. In the course of an intensive field survey of the flora of leeward Haleakala (Medeiros et al., 1986), we found fewer than ten seedlings and no saplings. Though numerous seeds are produced, their viability is often low, and predation on seeds by rodents may occur.

Ranunculus mauiensis and *R. hawaiiensis*

Two species of endemic Hawaiian buttercups (Ranunculaceae) were apparently fairly common in Haleakala Crater and vicinity at 1,800–2,800 m between 1840 and 1930. One species is apparently extirpated, and the other exists only in a few scattered populations. Cattle, goats, and pigs have undoubtedly played major roles in their decline. However, other factors seem to have influenced the dramatic decline of this genus in Hawaii in the past 60 years. A seedling of *R. mauiensis* from an ungulate-free site on West Maui was cultivated near Haleakala Park Headquarters (elevation 2,100 m). Herbivory that approached defoliation caused by alien slugs (*Milax gagates*) almost killed the young plant. After slugs were controlled, the plant recovered and grew to maturity.

FIGURE 5. *Plantago princeps*.

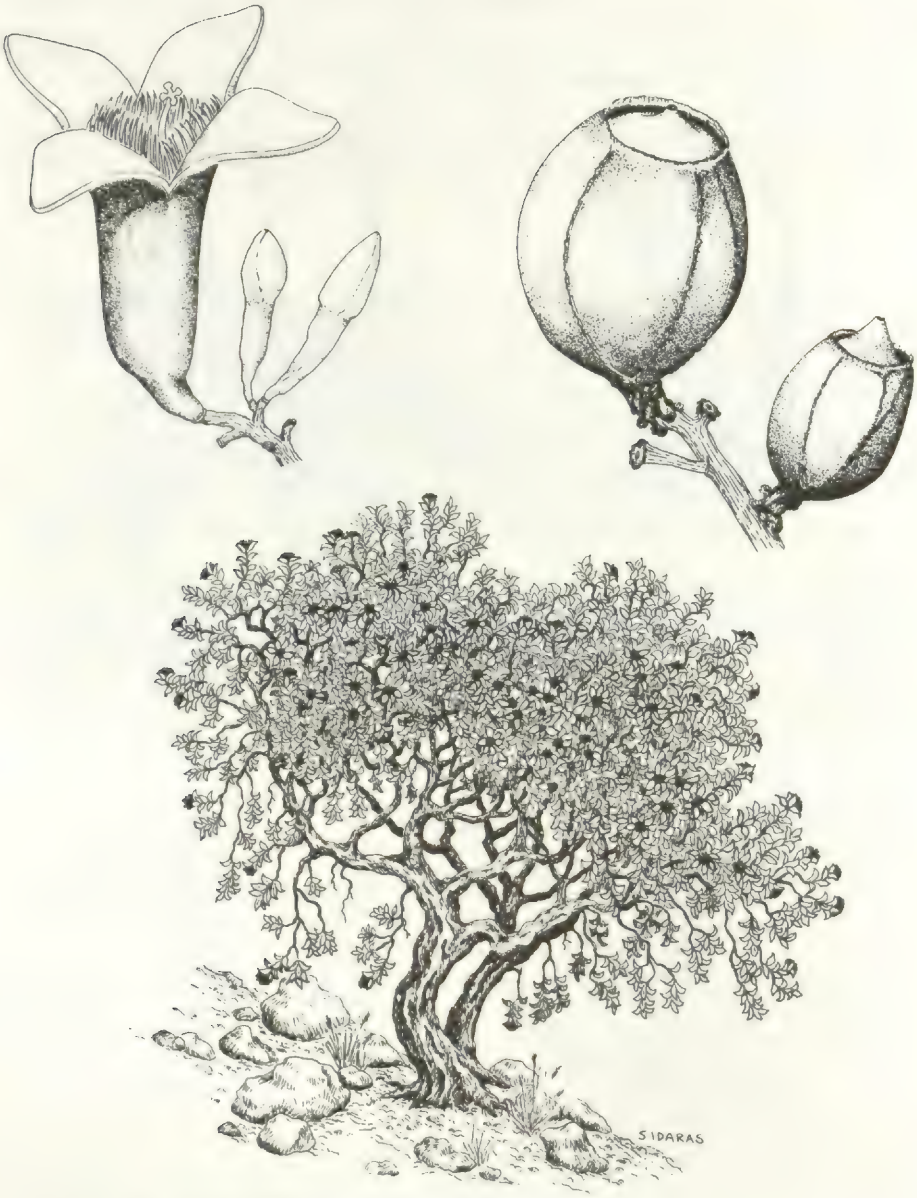

FIGURE 6. *Santalum haleakalae*.

Selective herbivory by alien slugs may be a significant factor in the decline of certain rare Hawaiian species.

Stenogyne

The Hawaiian mints (Lamiaceae), which include three endemic genera, make up another group that has proved highly vulnerable to feral ungulate damage. Of eight taxa of the endemic Hawaiian genus *Stenogyne* described for East Maui, five are believed extinct. The last collection of *Stenogyne haliakalae* in Haleakala National Park was made at 1,680 m elevation in dryland forest in 1937.

The vine *Stenogyne crenata* (Fig. 7) may once have been common in shrubland of upper Haleakala volcano. It now survives only in association with the canopies of the small trees *Sophora chrysophylla* and *Santalum haleakalae* that provide protection from feral goats. In *Sophora* forest in Haleakala Crater, from which goats have been excluded, *S. crenata* has made a modest recovery through seedling establishment and vegetative growth. Factors tending to retard recovery are a dense understory of alien velvetgrass (*Holcus lanatus*) and other competition in the lower 1.5 m of tree crown below the former goat browse level.

Stenogyne kamehamehae, with its 6–8-cm white or red corolla, and the smaller, white-flowered *S. rotundifolia* survive, growing terrestrially in upper-elevation sites undisturbed by pigs.

Platanthera holochila

Although Hawaii is famous for cultivating orchids (Orchidaceae), with over 1,000 species introduced from tropical areas throughout the world, the archipelago has only three native species of Orchidaceae. The impoverishment of the Hawaiian orchid flora has been attributed to failure of proper pollinators and/or proper symbiotic mycorrhizae to establish here. Two of the native orchids, *Anoectochilus sandvicensis* and *Liparis hawaiiensis*, occur somewhat rarely in rainforests of Haleakala National Park. The third species, *Platanthera holochila* (Fig. 8), was once fairly common in the Hawaiian Islands but has declined rapidly. This species was so abundant as recently as 1919 at one location (Lake Waianapanapa) within the park that the botanical explorer C. N. Forbes collected nine specimens (Forbes, 1919). Only three small populations are now known in the Hawaiian Islands. One of these occurs in shrubland at 2,000 m elevation just outside the boundaries of Haleakala National Park on reserve land managed by The Nature Conservancy. Observations of digging by pigs dangerously nearby led to enclosure of the orchids by a fence in 1984. The reason for the abrupt decline of this species is unknown, although many possible causes have been suggested: selective feeding by pigs, over-collecting by botanists, herbivory by slugs, an unknown orchid pathogen, and other possibilities.

Conclusions

Too little is known regarding the ecology, life histories, and breeding systems of Hawaiian plants. More research is desperately needed to improve this situation. Meanwhile, measures taken to mitigate the primary threat of feral ungulates in Hawaii's national parks (Stone & Holt, this volume) appear effective and essential for protecting the last remnants of our natural heritage in Hawaii. Most of us would agree that active management is necessary for preservation of areas of relatively intact biota of oceanic islands. Vulnerable island species depend on human action to protect them from the catastrophic effects of the biological invaders ironically brought in by humans. Simultaneously, it seems inevitable that new invaders will continue to appear in the future (Beardsley, 1979).

An example of the subtleties sometimes involved in the decline of insular systems is the vulner-

FIGURE 7. *Stenogyne crenata.*

ability of essential pollinators to alien predators. The Argentine ant (*Iridomyrmex humilis*) and western yellowjacket (*Vespula pensylvanica*) (Gambino et al., 1987) at Haleakala seem to have the potential for impoverishment of high-elevation insect faunas, which have remained largely intact until now. In the case of these two aliens, we feel that through careful control efforts there may be real opportunities to limit their effects. Sadly, prospects for appropriate intervention are generally too few. Often, restrictive funding situations prevent appropriate management actions from being

FIGURE 8. *Platanthera holochila*.

implemented. We feel, nevertheless, that better understanding of the biological interrelationships among native and alien species—competition, allelopathy, mycorrhizal relationships, nitrogen fixation, pollination, dispersal, seed predation, and herbivory—can contribute enormously to the conservation biology and management of oceanic islands.

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REVEGETATION ON BIKINI ATOLL, 1985

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Abstract

Bikini, a coral atoll in the Marshall Islands, Central Pacific, formerly covered by an anthropogenous vegetation of coconut palms, with an undergrowth of mostly native herbs and shrubs, was devastated and its vegetation largely destroyed by a series of nuclear bomb tests in the 1940s and 1950s. The present vegetation, studied in 1985, showed a remarkable recovery, having lost a few native species, but gained a substantial component of exotics not present before the testing program. Not only was the 1985 vegetation unexpectedly luxuriant, but a considerable number of species, both native and exotic, now attain a considerably greater stature than is commonly seen elsewhere. The notable resilience of the vegetation, perhaps because it is so poor in species, seems at present its outstanding feature.

The Marshall Islands make up a large archipelago, over 600 miles in longest dimension, northwest to southeast, lying in the west-central part of the Pacific Ocean (Fig. 1). They are about one-sixth the circumference of the Earth almost due west of the Galápagos, due north of New Zealand, and due south of the western part of the Bering Sea and the Aleutian Islands. The group comprises 28 coral atolls and six flat, single coral islands called table reefs. An atoll is a more or less irregularly necklace-shaped coral reef with from one to many relatively small, flat islets arranged on it, surrounding a relatively shallow body of water called a lagoon (Fosberg, 1957, 1960, 1962, 1976). Bikini, subject of this essay, is a fairly typical example of a coral atoll.

Atolls, because of their comparative lack of physiographic diversity, their relatively uniform limestone substratum, the prevalence of salt spray in their atmosphere, and probably a history of almost complete submergence since the end of the Pleistocene a few thousand years ago, have impoverished floras. These are composed principally of strand species. The indigenous vascular floras vary in number of species from one to perhaps 100, depending on amount and distribution of rainfall and degree of isolation from continental floras. Most of their species are widespread and salt-tolerant. Only a very few are endemic to coral islands and almost none are local endemics.

Their vegetation is also relatively simple, of a few types, some of them dominated by single species, a condition unusual in the tropics. Most of this original vegetation, on all but the driest atolls, has been converted by humans to coconut plantations, marshy depressions for taro cultivation, and villages. In the public imagination swaying coconut palms with long, graceful fronds are the characteristic vegetation of coral atolls. These are in no sense the original natural vegetation of these islands, but through the activities of humans they have become the actual vegetation of most atolls, including Bikini up to 1946.

Recent History

The first survey of the flora and vegetation of Bikini Atoll was made in 1946 by Taylor (1950). He reported 35 species of vascular plants, three of them weedy exotics, four (or possibly eight) of aboriginal introduction, and 29 (or possibly only 25) indigenous.

He described the then-existing vegetation but generalized his types for the four atolls that he visited: Bikini, Eniwetok, Rongelap, and Rongerik. Basically, the natural vegetation described is a scrub or small forest of *Scaevola sericea*, *Tournefortia argentea*, *Guettarda speciosa*, and *Suriana*

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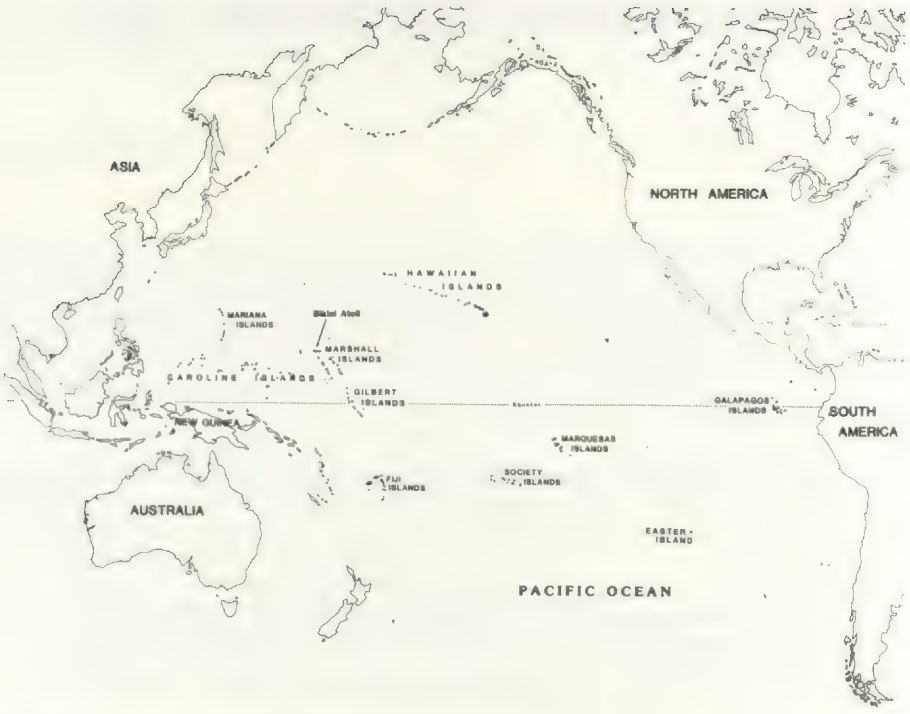

FIGURE 1. Outline map of Pacific Basin, showing location of Marshall Islands and Bikini Atoll.

maritima. Inland, this formed with some admixture of *Pisonia grandis* and *Ochrosia* (= *Neisosperma*) *oppositifolia*, a "woodland" or low forest, mostly mixed with planted coconuts. Just behind the beaches, this was more shrubby and nearly impenetrable, called by Taylor "marginal vegetation." He also described *Pisonia grandis* forest, local on less disturbed islets, a pure stand with almost no undergrowth, and dense *Cordia subcordata*, also inland and very prevalent on the largest islets. Local stands of *Pemphis acidula* also occurred. In most of these types, except *Pisonia* forest, the ground cover was a "coarse and rough turf" of a varying mixture of *Lepturus repens* and *Fimbristylis cymosa*.

His descriptions of the vegetation of the four atolls that he visited are mainly discussions of the distribution and variations of the above types and of their relations with the variations in soil texture and abundance or lack of organic matter or humus. Little resemblance, except on the coarsest scale, now remains to the patterns and arrangements described by Taylor.

After Taylor's visit in 1946, and at intervals until 1958, the vegetation was altered catastrophically by a series of nuclear bomb tests and by clearing for installations connected with the tests. No record was kept of the effects on the vegetation of these successive destructive events, but there is no doubt that the former structure and pattern were completely altered and that there was much absolute destruction. Most of the species, however, persisted.

Between 1958 and 1968 no observations of vegetation or collections of specimens were made, at least none were placed on published record.

In the late 1960s the Atomic Energy Commission decided that Bikini was safe enough radiologically for its exiled inhabitants to return to their former home. In preparation for this, the authorities caused coconut trees to be planted in a 30 × 30-foot geometrical pattern over the entire surface of

the two largest islets, Bikini and Eneu. Substantial non-Marshallese-style houses were built on Eniwetok Islet, and the people were brought back. It was not long before it became clear that, in spite of the optimism of the promoters of the scheme, radiation levels were too high for safe human habitation. The people were again removed and taken back to Kili Island and other places where they had settled. Nature was again allowed to take its course. Again no records were kept of the response of the vegetation. To the best of my knowledge, no vegetation specialist or other sort of botanist visited the atoll between the end of bomb-testing in 1958 and 1985. Shortly before the latter date, pressure built up to do something to decontaminate the atoll so the people could again return. A major series of investigations was initiated as to the feasibility of this. I was engaged to survey the condition of the vegetation and spent approximately three weeks on the atoll (Fosberg, 1987).

Description of Present Vegetation

I had expected some recovery and reestablishment of a vegetative cover but had no information even on the extent of the damage that had resulted from the testing program. I had, by chance, had a quick look at an air view of a part of one islet after the 1954 hydrogen bomb blast. The entire coconut palm population had been flattened to the ground.

So I was unprepared for the way the vegetation had come back. Even the smallest islets were densely covered by scrub and scrub forest. Larger islets were well forested.

Ten islets, covering the whole range of size from several hectares to Bikini, the largest, were visited and walked over, as well as the larger ones studied on color air photos. Lists of species and estimates of abundance, stature, and distribution were made on all islets studied, and reconnaissance vegetation maps of the three largest islets were made.

Of the original species recorded by Taylor in 1946, nine were missing or at least not found in 1985. Twenty-five additional species, not previously recorded, were found. Of these five or possibly six are native in the northern Marshalls. The rest are exotics, weeds, or persisting from cultivation.

No clear abnormalities of the plants were noted, though such were looked for. One peculiar feature was observed on the two largest islets. Here a large proportion of the native and exotic species reached a much greater stature than was usual in similar habitats on other atolls in the region. No convincing explanation of this phenomenon has occurred to me yet.

There was little evidence of pattern or orderliness in the distribution of the plant communities that had formed, and the definable communities were very simple. The amount of soil disturbance by explosions and bulldozing was such that any vegetation patterns depending on soil patterns were unrecognizable.

The coconut plantings on the two largest islets, presumably of approximately the same age, showed notable differences in vigor and color in different areas, probably reflecting differences in soil properties, but there was not time to do serious soil sampling or profile examination. Effects of wind and salt spray are evident on coasts exposed to the trade winds. Dwarfing and yellow color seem related to exposure.

Woody vegetation, other than coconuts, in exposed habitats is dwarfed and wind-sheared. On lee sides and in interiors luxuriance is notable. Certain tree and shrub species, such as *Pisonia grandis*, *Cordia subcordata*, *Dodonaea viscosa*, *Guettarda speciosa*, *Hibiscus tiliaceus*, *Clerodendrum inerme*, and *Morinda citrifolia*, are better developed and more common in the interiors of the larger islands, and even of some very small islets, than is usual in such habitats on similar atolls. The beach ridges, especially on the lagoon beaches, have a fairly characteristic, though by no means constant, assemblage of woody species, notably *Cordia subcordata*, *Tournefortia argentea*, *Suriana maritima*, and *Scaevola sericea*.

Fairly general but locally varied in species composition is a herbaceous ground cover of *Lepturus repens*, *Fimbristylis cymosa*, *Triumfetta procumbens*, *Boerhavia tetrandra*, *Boerhavia albiflora*,

Portulaca oleracea, Portulaca lutea, Portulaca australis, Thuarea involuta, and, very locally, *Paspalum setaceum.* In open areas on Bikini and Eneu, the grass *Eustachys petraea,* a recent immigrant in Micronesia from the Caribbean, was extraordinarily tall and abundant.

On the smaller islets, except those on the southwest reef, the vegetation is dense but very simple. These islets are mostly covered by a scrub or scrub forest of *Scaevola sericea* with an important component of *Tournefortia argentea* either as scattered emergent small trees, or a mixture, varying to dominant, of *Tournefortia argentea* and *Guettarda speciosa. Pandanus tectorius* and very rarely *Pemphis acidula* are scattered in this vegetation. *Suriana maritima* forms a fringe on lagoon shores locally. *Fimbristylis cymosa* fills small openings. *Ipomoea macrantha,* a tough vine, is tangled here and there in the bushes and trees.

Nam, the third-largest islet, on the northwest end of the atoll, is wide and should have some forest in the interior. However, it was close to the site of the "Bravo" hydrogen bomb test and lost its western peninsula. It is now densely covered by a scrub to scrub forest mixture of *Scaevola sericea* and *Tournefortia argentea.* The *Tournefortia* appears as emergents above the *Scaevola.* On the west side bordering the Bravo crater, a strip of scrub forest, predominantly *Tournefortia,* was dead at the time of our survey from no apparent cause.

On the southwest reef are six very small islets of different shapes that are commonly spoken of as "still in their natural condition." They are forested, largely by low closed-canopy stands of *Pisonia grandis,* a tree which elsewhere in the Marshall Islands, in old stands, has trunks of enormous diameter and reaches 30 m in height. Here on these tiny islets these trees have trunks seldom exceeding 25 cm diameter and reach about 10 m in height. There is almost no undergrowth in dominantly *Pisonia* stands. Around the peripheries are small stands of mixed *Tournefortia, Scaevola, Pisonia,* and *Guettarda.* The size range of the *Pisonia* forest, remains of heavy equipment, and the proximity to the Bravo test site suggest that this forest has developed since the end of the test program in 1958.

Discussion and Conclusions

The vigor and density of the present Bikini vegetation is a striking demonstration of vegetation dynamics and resiliency. The absence of clear patterns results presumably from the extreme disturbance of the substratum by the explosions, bulldozing, and coconut planting. No apparent genetic or physiologic effects of radiation were seen, unless the unusual stature of some of the species is in some way connected with these.

The recovery of vegetation after severe perturbations, such as nuclear explosions, clearing, and introduction of feral animals, observed on many islands, in cases where the causes of destruction or decline are removed, seems a general phenomenon. The resulting vegetation is not usually exactly what was there before, but if the seed stock of the indigenous species has not been destroyed, it may eventually approach its original state. Even total destruction of the vegetation, such as by a nuclear explosion, if seeds remain or if the same species still grow near enough for reinvasion to take place, is followed by reestablishment of a succession toward something similar to what was destroyed.

This capacity of vegetation to recover after perturbation, sometimes termed "resilience," is general enough to be a justification for efforts toward conservation, even in situations that seem quite discouraging, as in heavily damaged areas in Hawaii, the Galápagos, and even St. Helena. In most cases, though not precisely in Bikini, efforts should be directed toward understanding and removing the causes of the perturbation. In Bikini, conservation policies should be directed to protecting adequate samples of the recovering vegetation types as the atoll is rehabilitated for eventual reoccupation by the Bikinian people. Ill-considered and indiscriminate "improvement" can sometimes be as destructive to natural phenomena as are nuclear explosions. Such activities cannot be stopped on the atoll as a whole, but care should be taken to preserve areas of each

distinctive habitat type sufficiently large to be viable for continuing succession toward stable natural ecosystems. The descendants of the Bikinians and our own may not thank us for bequeathing to them nothing but artificial and contrived cultural landscapes, however comfortable and well-regulated these may be for continued but monotonous existence. Efforts to avoid this latter calamity are an important part of what conservation is all about.

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THE WORLD CONSERVATION MONITORING CENTRE AND THREATENED ISLAND FLORAS

Stephen D. Davis[1]

ABSTRACT

The work of the Threatened Plants Unit of the World Conservation Monitoring Centre and the Botanic Gardens Conservation Secretariat is described. Data are presented on the current status of a number of oceanic island floras. Latest statistics show that 62% of the endemic plants of the Galápagos are either rare or threatened according to IUCN criteria. A survey of approximately 250 botanic gardens revealed that only 18 threatened plant taxa of the Galápagos are in cultivation. The ways in which conservation data can be used to support in situ and ex situ conservation are discussed, and current developments of the WCMC database are reviewed. These include the further development of the Plant Conservation Bibliography database, a proposed database on invasive species, and the preparation of a directory and conservation strategy for some of the world's most important botanical sites.

The Joint IUCN–WWF Plant Advisory Group estimated in 1985 that as many as 60,000 plant species could become extinct by 2050 if present trends continue. This would represent the greatest loss of plant species ever to occur during such a short time. The situation is made more urgent when the global distribution of endangered species is taken into account. Most losses will no doubt occur in very vulnerable, species-rich habitats, such as tropical forests and wetlands, and on oceanic islands with high endemism. In tropical forests alone, we may be losing at least one plant or animal species per day through disruption or conversion of forest to various uses (Myers, 1979). The floras of many oceanic islands are acutely threatened too. For example, at least 10% of the flora of Hawaii is already extinct and about 30% threatened (Sohmer & Gustafson, 1987). Ninety-six percent of the endemic flora of Rodrigues and of St. Helena is either rare or threatened. The plight of the Galápagos flora is no less serious: latest IUCN statistics (May 1987) indicate that 62% of endemic taxa are either rare or threatened according to IUCN Red Data Book categories.

Action to conserve plant species, whether in situ or ex situ, requires accurate and timely information on which to base decisions. IUCN (the International Union for Conservation of Nature and Natural Resources) set up the Conservation Monitoring Centre (CMC) in 1983 to provide such an information service for global conservation. In 1988, CMC became the World Conservation Monitoring Centre (WCMC), supported by IUCN, the United Nations Environment Programme (UNEP), and the World Wide Fund for Nature (WWF). The primary function of WCMC is the continuous collection, analysis, interpretation, and dissemination of information as a basis for conservation action. WCMC has the ability to assess and link the data on many thousands of species and areas. It carries out its function by integrating four Units, which hold conservation data on plants, animals, protected areas, and wildlife trade. Data from each Unit are linked by common geographical and taxonomic coding systems via a Wang VS computer. Data are stored in data files, permitting rapid processing and analysis, and as text files. Computerized information is backed up by manual files. Table 1 provides a summary of the units comprising WCMC, and Table 2 is a list of some of their major outputs.

The users of WCMC include the planning and programming divisions of IUCN and WWF, governments, governmental agencies, and nongovernmental organizations that make up the mem-

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TABLE 1. The components of the World Conservation Monitoring Centre (WCMC) and IUCN's Botanic Gardens Conservation Secretariat (BGCS).

Data files	Text files	Manual files
PROTECTED AREAS DATA UNIT		
10,500 protected areas (mainly above 1,000-ha areas)	Detailed text files on ca. 4,500 protected areas; management plans	Maps National park brochures
SPECIES CONSERVATION MONITORING UNIT		
Summary information on 18,000 animal taxa of conservation concern (70,000 taxon distribution records)	Detailed Red Data Book accounts on ca. 2,500 animal taxa	Correspondence Books and reports
WILDLIFE TRADE MONITORING UNIT		
Type and quantity of shipments of endangered taxa and their products imported and exported under CITES; ivory trade data (ca. 160,000 records)	Reports and information sheets on taxa or groups; accounts of types of trade (ca. 5,000,000 records) and wildlife utilization activities	Annual CITES trade statistics and reports on wildlife
THREATENED PLANTS UNIT		
Summary information on 43,000 plant taxa of which 18,000 world threatened; Data from 67 Red Data Books covering 17,000 records of 12,000 plant taxa; 10,000 plant conservation references	Detailed Red Data Book accounts on ca. 5,000 plants; summary data on areas and centres of plant diversity	Correspondence, books, reports, threatened plant lists
BOTANIC GARDENS CONSERVATION SECRETARIAT		
File of 1,300 botanic gardens; records of 5,000 threatened taxa in cultivation	Reports on plants in cultivation	Garden brochures

bership of IUCN, as well as international developmental banks, aid agencies, and the media. WCMC also provides information on conservation to the Global Environment Monitoring System (GEMS) of the United Nations Environment Programme (UNEP). Various aspects of the work of WCMC have been described by Lucas & Synge (1981, the development of plant data), Harrison (1983, protected areas), and Mackinder (1983, 1984, development of the overall database).

THE THREATENED PLANTS DATABASE

The Threatened Plants Unit (TPU) of WCMC maintains a computer data file that began as an index of threatened plant species. It now covers nearly 43,000 accepted plant taxa of conservation concern with their full distributions. So far, 18,000 plant taxa have been identified as rare or threatened on a world scale using the IUCN Red Data Book categories to measure the degree of threat to wild populations. Most of these records are of plants from temperate regions and islands, where the floras are generally better known than those of continental tropical areas. The aim is that the file should eventually include *all recorded* world threatened plants, and this target has almost been reached. Other records in the database include plants that are threatened in one country but are

TABLE 2. Major outputs of WCMC.

PROTECTED AREAS
IUCN Directory of Afrotropical Protected Areas (1987)
IUCN Directory of Indomalayan Protected Areas (in prep.)
IUCN Directory of Neotropical Areas (1982)
The 1985 United Nations List of National Parks and Protected Areas
ANIMALS
IUCN Red Data Book series on animals:
Amphibia–Reptilia, Part 1 (1982)
Invertebrates (1983)
Mammals, Part 1—The Americas and Australasia (1982)
Threatened Birds of Africa and Related Islands, Part 1 (with ICBP) (1985)
Threatened Swallowtail Butterflies of the World (1985)
IUCN Red List of Threatened Animals (1986)
UNEP/IUCN Directory of Coral Reefs of International Importance—1: Atlantic and eastern Pacific (1986)
WILDLIFE TRADE
IUCN/CITES Directory of Crocodilian Farming Operations (1985)
Traffic Bulletin (quarterly)
Comparative tabulations and reports on trade in wildlife products by country and/or animal or plant group
PLANTS
The IUCN Plant Red Data Book (1978)
Plants In Danger: What Do We Know? (1986)
Centres of Plant Diversity (in prep.)
Threatened Plants Newsletter (twice yearly)
Lists and reports on threatened plants
BOTANIC GARDENS
Botanic Gardens Conservation Secretariat: a Prospectus (1987)
Botanic Gardens Conservation Strategy (in prep.)
Botanic gardens lists and reports of plants in cultivation

of unknown status or are safe in another, species that are being screened and have been found to be safe (i.e., in the IUCN category "not threatened" or "nt"), and complete checklists of certain plant groups of conservation concern (e.g., palms, cycads, tree ferns, cacti, and the endemic floras of many islands, such as that of the Galápagos). For each plant we record its full scientific name with authority, distribution, and conservation status. Distribution is mainly recorded at country or state levels with geographical qualifiers to refine the data. It is intended that habitat data will be added to the data file in the near future. Conservation status is recorded at world, regional, and country/state levels, using the IUCN categories. More data are available in computerized text files on about 500 species.

Since the publication of *The IUCN Plant Red Data Book* (Lucas & Synge, 1978), which gave examples of just 250 threatened plants from around the world, there has been an enormous wealth of literature published on threatened plants worldwide. Threatened plant lists and Plant Red Data books have been prepared for many countries and islands. The contents of each national Plant Red Data Book are entered into the computer along with information about the content of the book and the data it contains. A conversion table allows IUCN Red Data Book categories for individual species to be entered alongside these categories assigned in the book. Normally, the conversion is automatic, but if there is any data loss, this is recorded. Other fields indicate whether the plant is native or introduced to the area concerned. A plant-data-viewing program allows summary data for an area to be displayed, together with data from the Plant Red Data books from which that summary was made. So far 67 (mainly European) Plant Red Data books have been entered into this part of the database, covering 17,000 records of 12,000 plant taxa.

TABLE 3. Endemic vascular plant taxa from selected oceanic islands. Ex Extinct; Ex/E Possibly extinct; E Endangered; V Vulnerable; R Rare; I Indeterminate; K Insufficiently Known; ? no data; nt not threatened.

	Ex	Ex/E	E	V	R	I	K	?	nt	Total	Rare or Threatened[1]
Azores	1	—	—	5	18	6	—	11	14	55	30 (55%)
Canary Islands	1	—	128	134	145	7	—	39	176	630	415 (66%)
Galápagos	2	—	11	12	105	12	2	3	83	230	142 (62%)
Juan Fernandez	1	—	52	32	10	1	—	17	6	119	96 (81%)
Lord Howe	—	—	2	10	58	3	—	1	2	76	73 (96%)
Madeira	—	—	16	30	39	—	—	22	23	130	85 (65%)
Mauritius	18	1	65	35	39	14	—	11	39	222	172 (77%)
Seychelles[2]	—	6	17	9	2	38	—	18	—	90	72 (80%)
Socotra	1	—	84	17	29	1	—	2	81	215	132 (61%)

[1]Categories Ex + Ex/E + E + V + R + I.
[2]Granitic islands only; excludes Aldabra.

In order to provide an overview of what is known about the status of the flora of each country around the world, TPU compiled a book entitled *Plants in Danger: What do we know?* (Davis et al., 1986). For each country or island group the book provides information on the size of floras; the number of endemic taxa and other statistics on threatened plants; and references to major checklists and floras, Red Data books, and important plant conservation references. The addresses of botanic gardens and organizations involved in plant conservation are also listed. Table 3 (adapted from Davis et al., 1986) lists islands with between 50 and 1,000 endemics where over 75% of the flora have been assigned to one of the IUCN Red Data Book categories.

Some smaller islands, such as St. Helena, have been devastated by introduced animals, notably goats. They were introduced to that island in 1513 and have been the main threat to the flora. Today, 47 endemics (96% of the endemic St. Helena flora) are either rare or threatened; 7 are already extinct and 23 endangered. There is still time to prevent such colossal damage to the flora of the Galápagos Islands.

Monitoring Threatened Species

Having identified which species are under threat, the next logical step is to set up a regular monitoring and documentation system at a national or local level. This is the idea behind the planned "Plantwatch" scheme, in which local botanists would visit the sites of chosen species to assess the status of each population on a regular basis.

Information from field survey forms could be maintained on a PC system and would provide early warning to indicate threats and conservation needs, as well as to show the effectiveness of existing conservation measures. Such a system would work well on islands such as the Galápagos, where the floras are relatively well known and the number of species not unduly large. A number of fundamental biological issues need to be resolved before a system is set up (e.g., the frequency of field visits), so it is planned to hold a workshop in the near future to develop the methodology and provide guidelines for "Plantwatch" schemes.

Monitoring ex Situ Conservation

In some cases it may be already too late to ensure that viable populations of threatened plants survive in the wild. In these cases, ex situ conservation is now the only option available. Knowing which plants are threatened in the wild means WCMC can also monitor their status ex situ,

principally in botanic gardens. This has been the work of IUCN's Botanic Gardens Conservation Co-ordinating Body and will be continued and expanded by the newly established Botanic Gardens Conservation Secretariat. The "Body," set up at a conference at Kew in 1978, had around 250 gardens that were members or associated with its work. Lists of threatened taxa of particular regions or families were circulated to botanic gardens, which were asked to annotate them with their holdings. Information from the returns is held on computer by WCMC, and reports can be prepared on which threatened plants are in cultivation and who is growing them. "Garden printouts" can also be made listing, for each garden, all the conservation plants recorded by that garden, their distribution and IUCN Red Data Book category, the source of their holdings, and the number of other gardens growing that plant. Such printouts can be especially useful to botanic garden curators who need to assess the conservation value of their holdings. Priority plants for bulking up and distributing to other gardens can be highlighted.

Up to the end of 1986, threatened plant lists had been circulated covering most of the temperate zone and subtropics as well as some parts of the tropics. Lists of rare and threatened plants of the Galápagos were circulated to gardens in 1983, and a report on garden holdings of Galápagos endemics was subsequently prepared (IUCN, 1984a). Latest statistics show that out of 151 rare or unthreatened taxa listed in 1983, only 18 taxa (11%) are known to be in cultivation in 12 gardens worldwide. Of those taxa represented in cultivation, 12 (67%) are known to be in only one botanic garden. A full list of Galápagos taxa known to be in cultivation, and the botanic gardens growing them, is given in Table 4.

The new Botanic Gardens Conservation Secretariat (BGCS), set up on 1 January 1987, will continue to coordinate conservation activities of botanic gardens worldwide. This follows from the Joint IUCN–WWF Plants Conservation Programme, which included botanic gardens as one of six theme areas, and a conference on Botanic Gardens and the World Conservation Strategy in November 1985 at Las Palmas, Canary Islands. BGCS, which is under the direction of Vernon Heywood, runs in close association with TPU, with which it shares offices at Kew. The aims of the Secretariat are: to promote the implementation of a botanic gardens conservation strategy (Heywood, in prep.); to monitor and coordinate ex situ collections of plants worthy of conservation; to develop programs for liaison and training; and to arrange a Botanic Gardens Conservation Congress every three years. Details of the Secretariat's activities and an invitation for gardens to subscribe to the scheme can be found in *Botanic Gardens Conservation Secretariat: A Prospectus* (IUCN, 1987).

WCMC and National Plant Conservation Databases

The development of an overview plant conservation database on the conservation status of plants in situ and ex situ has up to now been the main focus of WCMC's plant activities. However, it is clearly unrealistic for WCMC to hold a comprehensive set of conservation data for all plant taxa. Furthermore, the needs of plant conservation at national or local levels can best be answered by specialist databases. Most decisions in conservation are local and national, rather than international. Already national Conservation Data Centres (CDCs) have been set up by The Nature Conservancy, and others are planned at country level (e.g., in Malaysia) or are being developed for individual protected areas and botanic gardens. In addition, there are databases dealing with special subject areas, such as economic plants and taxonomy.

Increasingly, WCMC is being asked to provide guidelines on both the conceptual framework and minimum data elements necessary for national plant conservation and other specialist databases and to develop International Transfer Formats to standardize data exchange via computer links among countries and with WCMC's global overview database. These developments were outlined by Mackinder & Synge (1986) and Leon (1986). We see the WCMC plant database emerging as an overview of other databases, rather than trying to hold every fact relevant to plant conservation, so

TABLE 4. Botanic gardens list of rare and threatened taxa of the Galápagos.

AMARANTHACEAE	
Pleuropetalum darwinii Hook. f.	B[2], BERN, *U*+[1,4]
CACTACEAE	
Jasminocereus thouarsii (F.A.C. Weber) Backeb. var. *thouarsii*	u[3]
Opuntia echios J. Howell var. *echios*	*AAU*[1], *U*
Opuntia echios var. *barringtonensis* E. Dawson	*K*[1]
Opuntia echios var. *gigantea* (J. Howell) D. Porter	*HNT* +[1,4], *K*[1]
Opuntia echios var. *zacana* (J. Howell) E. F. Anders. & Walk.	*U*[1]
Opuntia galapageia Henslow var. *galapageia*	B[2], ZSS
Opuntia megasperma J. Howell var. *megasperma*	*U*[1]
Opuntia megasperma var. *orientalis* (J. Howell) D. Porter	*HNT*[1]
CONVOLVULACEAE	
Ipomoea tubiflora Hook. f.	BATU[2]
ERICACEAE	
Pernettya howellii Sleumer	SUCH[2]
EUPHORBIACEAE	
Acalypha flaccida Hook. f.	SUCH[2], TBI
Acalypha velutina Hook. f.	AA[2]
Croton scouleri Hook. f. var. *brevifolius* (Andersson) Müll. Arg.	AA[2], TBI
Croton scouleri var. *grandifolius* Müll. Arg.	TBI[2]
MYRTACEAE	
Psidium galapageium Hook. f. var. *howellii* D. Porter	*SDZO*[1]
PIPERACEAE	
Peperomia galapagensis Hook. f. ex. Miq. var. *ramulosa* (Andersson) Yuncker	TBI[2]
Peperomia petiolata Hook. f.	TBI[2]

Index of Botanic Garden Codes

AA	Main Botanical Garden, Kazakh Academy of Sciences, 480070 ALMA-ATA, Kazakh S.S.R., U.S.S.R.
AAU	University of Åarhus Botanical Institute, 68 Nordlandsvej, DK-8240 Risskov, Denmark.
B	Botanischer Garten und Museum Berlin-Dahlem, Konigin-Luise-Strasse 6-8, D-1000 Berlin 33, Federal Republic of Germany.
BATU	The Botanical Garden, Georgian Academy of Sciences, Machindzauri, 384533 Batumi, Georgia S.S.R., U.S.S.R.
BERN	Botanischer Garten der Universitat Bern, Altenbergrain 21, CH-3013 Bern, Switzerland.
HNT	Huntington Botanical Gardens, 1151 Oxford Road, San Marino, California 91108, U.S.A.
K	Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, U.K.
SDZO	San Diego Zoological Garden, P.O. Box 551, San Diego, California 92112-0551, U.S.A.
SUCH	Sukhumi Botanical Garden, Georgian Academy of Sciences, Chavchavadze Street 20, 384933 Sukhumi, Abkhazskaya, U.S.S.R.
TBI	Botanical Garden, Central Academy of Science, 380005 Tbilisi P.O. 5, Georgia S.S.R., U.S.S.R.
U	Botanical Gardens of the State University, Harvardlaan 2, Postbus 80-162, 3508 TD Utrecht, The Netherlands.
ZSS	Stadtische Sukkulenten-sammlung Zurich, Mythenquai 88, CH-8002 Zurich, Switzerland.

[1]Capital italic indicates plants from a known wild source.

[2]Capital Roman indicates plants from a known cultivated source. Where a garden holds both wild and cultivated source material, the code to indicate known wild source is used as, clearly, the wild source material is the more valuable.

[3]Lowercase indicates plants from an unknown source.

[4]+ following the code indicates that duplicate material is available.

that a certain minimum level of data is held on all threatened plants or countries with pointers to more detailed information. The WCMC database can then be used for comparisons among country data and for filling gaps where there are no national databases. National plant databases are in a way the logical step forward after the preparation of a Plant Red Data Book or threatened plant list and may be particularly apt for certain island floras, such as the Galápagos, where the effectiveness of conservation projects could be enhanced by regular monitoring of threatened plant populations.

The Plant Conservation Bibliography

An important part of the WCMC database, as it emerges as an overview on conservation worldwide, is the bibliographic database, at present containing about 12,000 citations on references to plant conservation. This has developed from the Kew Conservation Current Awareness List. Since 1979 the Library of the Royal Botanic Gardens, Kew, has extracted references on plant conservation for TPU. In addition, the computer file has been expanded recently by search requests from a number of commercial databases. Entries are cross-referenced by subject (threatened plants, protected areas, economic plants, law, botanic gardens), by plant family, plant name, and geographical area. There is a detailed set of criteria for adding new references to the database, with the intention that the bibliography may eventually be published.

The datafile is also used for adding data sources for information in the threatened plant and botanic gardens datafiles. The intention is that all record fields for plant records will be cross-linked to the bibliographic database so users will know exactly the sources of each piece of information. Internal datasources (e.g., floras used for plant distribution records, personal communications, or returned questionnaires giving, say, details of conservation categories for particular taxa) can be sorted using an ACCESS field, so these will not appear in the published bibliography.

Centres of Plant Diversity

Although the WCMC database holds information on some 18,000 threatened plant taxa, for the vast majority of species it is not possible to assess their chances of survival, due to incomplete knowledge of their distributions, ecology, and population structures. Also, in many tropical areas there is simply not enough time to identify and gather information on individual threatened plant taxa. Furthermore, even if threatened species can be identified, it is not practical for governments or other bodies to set up reserves to cover thousands of species. The only workable solution is to establish large protected areas to save the world's most important plant sites.

TPU and the Joint IUCN–WWF Plants Conservation Programme are therefore preparing a book to be called *Centres of Plant Diversity—A Guide and Strategy for their Conservation*. The book will include accounts on about 150 areas on a global scale considered by botanists of highest priority for plant conservation. The emphasis will be on plant-rich areas of the tropics and oceanic island floras, including the Galápagos Islands. The intention is to present the book to conservation organizations and aid agencies to help direct the aid they offer toward conserving sites.

Invasive Species

One further development is a planned expansion of the database to cover "threatening plants" (i.e., invasive species) in addition to threatened plants. This was the subject of a meeting convened by the Scientific Committee on Problems of the Environment (SCOPE) on the Ecology of Biological Invasions held in Honolulu, November 1986, at which V. H. Heywood presented an overview entitled "Patterns, Extents and Modes of Invasions by Terrestrial Plants."

The number of plant species that can be categorized as invaders is impossible to assess accurately, perhaps on the order of 5,000–10,000; the extent of their invasions varies widely and is most marked where humans have acted as agents of dispersal, either accidentally or deliberately, through clearance for agriculture, grazing, or urbanization, with the introduction of cultivated species and often their accompanying weed flora.

Types of vegetation that are particularly affected include temperate and tropical grasslands and pastures, tropical dry and humid forests in accessible areas, island floras, and the vegetation in areas with a Mediterranean climate (e.g., the Mediterranean basin, South Africa, Australia, Chile). A disturbing trend has been the devastating effect of woody invaders in areas such as the Cape region, especially the fynbos. Woody plants of Australian origin, such as wattle and acacias, *Hakea* species and eucalypts, as well as Mediterranean pines, are invading and replacing the natural vegetation. In the Galápagos, *Cinchona succirubra, Lantana camara,* and *Psidium guajava* are among the most serious woody invaders that threaten native and endemic species.

A critical need is a comprehensive database of known and potential invaders, listing their identities, natural distributions, secondary distributions, and invasive properties, as well as references (including those on secondary carriers). SCOPE has expressed an interest in the development of an invasive species database, and a grant from WWF has allowed TPU to undertake a feasibility study on such a database.

In some parts of the world, ecosystems are more threatened by alien species than by direct disruption of their habitat by humans. It is important to be ahead of the invaders by being able to predict where and when the next invasions are likely to take place and by which species. It is also vital to know what measures can be taken to ensure eradication or control. The invasive species database could provide some of the answers to lessen the impact of invasive plants.

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PLANT CONSERVATION PRIORITIES WORLDWIDE—THE IUCN–WWF APPROACH[1]

Ole Hamann[2]

ABSTRACT

In 1984, the International Union for Conservation of Nature and Natural Resources (IUCN) and the World Wide Fund for Nature (WWF) initiated an international Plants Conservation Programme designed "to assert the fundamental importance of plants in all conservation activities." Based on the principles of the World Conservation Strategy, the Plants Conservation Programme aims at formulating, promoting, and supporting efforts to conserve plants, vegetation, plant genetic resources, and plants of demonstrated or potential economic value, particularly in the tropics. The six main objectives of the Programme and related activities are presented and discussed. The lessons learned from three years' activities on an international scale are discussed as a possible model for developing a comprehensive plant conservation program in the Galápagos Islands.

THE INTERNATIONAL UNION FOR CONSERVATION OF NATURE AND NATURAL RESOURCES (IUCN)

The IUCN was established in 1948 and is the leading independent organization concerned with conservation. The headquarters in Switzerland serves as secretariat for the union of 568 member organizations from 116 countries. The membership is composed of three categories: (1) states and government agencies. There are 57 state members and 126 government agencies, which usually are ministries or government-run organizations; (2) national nongovernmental organizations, which, with 342 members, comprise most of the IUCN family; and (3) international nongovernmental organizations, with 27 members. In addition, 16 conservation organizations are affiliate (nonvoting) members of IUCN.

The mixed membership of IUCN gives it the flexibility and independence of a nongovernmental organization, and it gives credibility and access in government circles. The membership includes virtually all the major national and international conservation bodies of the world.

Over 1,500 experts support the work of IUCN's six commissions: ecology, environmental education, environmental planning, environmental policy, law and administration, national parks and protected areas, and the survival of species. Their voluntary contributions of time and expertise allow IUCN to keep the world's environmental situation under review and to work out new approaches to the solution of conservation problems.

The IUCN secretariat conducts or facilitates IUCN's major functions: monitoring biological data and the status and trends of resources requiring conservation; developing plans, such as the World Conservation Strategy and the Botanic Gardens Conservation Strategy; supporting action arising from these plans by governments or other appropriate organizations; and finding ways and means to implement them.

The IUCN secretariat provides, for example, the major input into the programming of WWF's conservation activities around the world, serves as the secretariat for the Ramsar Convention

[1]From May 1984 to July 1987 I was responsible for the IUCN–WWF Plants Conservation Programme. It is a great pleasure to acknowledge the support of these two organizations to plant conservation in general and to the Galápagos Islands in particular.

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(Convention on Wetlands of International Importance, Especially as Waterfowl Habitat), and serves as technical advisor to the World Heritage Convention. IUCN's operational capability is assured through its three specialized centers: The Conservation Monitoring Centre (CMC), which gathers all data relevant to the status and trends of living natural resources; the Environmental Law Centre (ELC), which provides technical assistance in the drafting and review of resource-related legislation, such as the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES); and the Conservation for Development Centre (CDC), which operates field projects, mainly with development aid agencies, such as the Swedish International Development Authority (SIDA), the Canadian International Development Agency (CIDA), the Norwegian Agency for International Development (Norad), and others.

The World Wide Fund for Nature (WWF)

The WWF is a private, international conservation foundation with 23 affiliated, national organizations throughout the world. Its scope is the conservation of nature and the natural environment in all its forms: fauna, flora, landscape, soils, water, air, and other natural resources. WWF mobilizes on a worldwide basis the strongest possible moral and financial support for safeguarding the living world and seeks to convert such support into action based on scientific priorities. WWF ensures that its program has a sound scientific basis by collaborating closely with IUCN.

Since its founding in 1961, WWF has channeled over 110 million dollars (U.S.) into more than 4,000 projects in some 130 countries. These projects have saved many animals and plants from extinction and helped to conserve natural areas all over the world. WWF has served as a catalyst for conservation action, brought its influence to bear on critical conservation situations, and provided a link between conservation needs, the scientific resources necessary to meet them, and the governments and other authorities concerned.

The World Conservation Strategy

The basic philosophy underlying the work of IUCN and WWF is expressed in the World Conservation Strategy (IUCN/UNEP/WWF, 1980), where conservation and development are closely linked. The World Conservation Strategy defines conservation as "the management of human use of the biosphere so that it may yield the greatest sustainable benefit to present generations while maintaining its potential to meet the needs and aspirations of future generations."

The major objectives of conservation reflected in the World Conservation Strategy are: (1) to maintain essential ecological processes and life-support systems; (2) to preserve genetic diversity; and (3) to ensure that any utilization of species and ecosystems is sustainable.

The World Conservation Strategy recognizes that development is based on the modification of the biosphere and the application of human, financial, living, and nonliving resources to satisfy human needs and improve the quality of human life. It also recognizes that development is built on a foundation of natural resources, and the wise use of these resources to improve human welfare is the principal objective of development. At the same time, it recognizes that the absence of development is one of the major sources of environmental stress, thereby rendering conservation without development in the long run.

The gravest challenge facing mankind today is the irreversible reduction of the planet's capacity to support people. Some major causes for this, of concern to conservation and development alike, are based on the excessive and increasing demands placed on the world's natural resources. Millions of people in developing countries are compelled through short-term needs to destroy the resources necessary to free them from poverty in the long term. Huge areas of natural habitats are being lost, especially in tropical countries and on islands, resulting in loss of genetic diversity, species, and

ecosystems, and in a breakdown of ecological processes. In addition, deforestation and poor land management cause the loss of millions of tons of soil every year. This continuing depletion of natural resources will have adverse consequences reaching far beyond those countries where these resources are located.

The essential linkage between conservation and development can be illustrated by the problems facing Tegucigalpa, the capital of Honduras, with respect to its water supply. Tegucigalpa is one of the Central American cities that has the most rapid growth. The immigration is largely due, like in other capitals of developing countries, to environmental degradation and inequitable land tenure in the rural areas. Tegucigalpa's drinking water is mainly drawn from the forested hills surrounding the city, but the city authorities are unable to keep up the demand. As dry season deficit grows, civil disturbances become increasingly frequent. Half of the city's water originates in a cloud forest designated as a National Park, where it is collected directly from the streams, and where gravity gives the energy for transportation. Yet, because it is a National Park, and therefore low in terms of development priorities, the forest is invaded from all sides and its capacity to produce water is undermined. Now, should this forest be protected as a conservation priority because it is a priceless natural resource containing a cloud forest with unique species of plants and animals? Or should it be protected as a development priority as the main and cheapest source of the city's drinking water? In such a case there seems to be little difference.

The Plants Conservation Programme

Because of the accelerating worldwide deterioration of natural habitats, entire ecosystems may disappear, and as many as 60,000 plant species may become extinct before the middle of the next century, should present trends continue (IUCN–WWF Plant Advisory Group). The loss of biological diversity and genetic resources, specifically plant genetic resources, is a threat to the global life-support system. Should tens of thousands of plants disappear forever, it would amount to a fundamental and permanent change in the character of life on earth. IUCN and WWF recognize the problems involving the utilization of natural resources by humans and assert that such usage can be managed compatibly with conservation of these resources. Accordingly, IUCN and WWF aim at achieving the practical implementation of the objectives of the World Conservation Strategy.

This is the context in which the Plants Conservation Programme was launched in March 1984 to promote more effective plant conservation around the world, emphasizing particularly tropical plants and vegetation, and plants of demonstrated or potential economic value (IUCN & WWF, 1984). There was a strong sense that plants had been neglected in conservation and that the arguments for their conservation were stronger than those for more traditional animal-oriented conservation. The need to establish a scientific and institutional foundation to ensure a prominent place for plants on the conservation agenda was realized. The Programme was seen as offering a unique opportunity to bridge the gap between scientists, protected-area managers, and conservationists on the one side, and foresters and agronomists on the other, in the common cause of saving plant life.

Three years since the Programme was launched much of the scientific and institutional foundation is now in place, and substantial activities and projects have been initiated (Table 1) at a total investment of some two million dollars (U.S.), about three-quarters of which the WWF raised. To this figure should be added a larger one allocated to a range of projects under the Tropical Forest Programme, by which the conservation of plant-rich sites have been supported. There are two types of projects in the Plants Conservation Programme, both catalytic in emphasis: (1) strategic projects designed to develop the concepts and methodologies of plant conservation and to make them widely available; and (2) selected field projects in high-priority areas to apply the concepts and to act as models for others to follow.

TABLE 1. IUCN–WWF Plants Conservation Programme project list, July 1987.

Status	Project number[1]	Title
Completed	9076	Collaboration with FAO on international undertaking on genetic resources.
	9134	Poster on wild plant genetic resources for crop improvement with IBPGR.
	9146	Case studies on in situ conservation of plant genetic resources, with FAO. For booklet to be published by FAO in collaboration with members of the Ecosystems Conservation Group.
	9204	*Plant Sites Red Data Book*, Phase 1.
Ongoing	9200	Book on *Plant Conservation—Principles and Practice*, jointly with WWF (3329).
	9201	International consultation on the conservation of medicinal plants, with WHO.
	9202	Establishment and development of the Botanic Gardens Conservation Secretariat.
	9203	"List of Economic Plants for Conservation and Development."
	9206	Minimal databases on plant genetic resources in selected biosphere reserves.
	9222	Conservation of wild fruit trees, Malaysia.
	9262	Template textbook on biology.
	9263	Conservation in situ of *Phaseolus* in Latin America.
Completed	3121	International, development of Plants Campaign.
	3147	International, survey of activities of international organizations.
	3160	Assistance to India in the development of legislation to implement CITES.
	3198	International, tracking and analysis of politics of gene resources.
	3234	International, in situ gene banks for maintenance of wild genetic resources in tropical forest countries.
	3300	India, development of plants program.
	3303	International, collaboration with the Organization for Economic Cooperation and Development (OECD) on plants of pharmaceutical interest.
	3306	*Plants Programme* booklet.
	3309	Indonesia, medicinal plants of Gunung Leuser.
	3314	Spain, protection of endangered plant species.
	3316	Sierra Leone, botanical survey of Gola.
	3317	Portugal, conserving the flora of the Azores.
	3318	International, sponsorship of conference on botanic gardens and the World Conservation Strategy.
	3319	*Plants in Danger—What do We Know?*
	3322	Latin America, economic botany and threatened palms.
	3324	Yemen, botanical survey of Socotra for plant genetic resources.
	3655	Ecuador, rehabilitation program for Isabela Island, Galápagos.
Ongoing	3090	International, strategy for botanical inventory, tropical rainforests.
	3149	Mauritius, plant conservation.
	3301	International, operation of IUCN–WWF Plant Advisory Group.
	3304	Indonesia, medicinal plants of Siberut Island.
	3305	Southeast Asia, wild mango conservation.
	3307	Sri Lanka, consolidation of protection of the Sinharaja Forest.
	3308	India, plant conservation education program for youth.
	3310	Brazil, plant species threatened with extinction.
	3311	Brazil, studies of campo rupestre vegetation.
	3312	International, plant protection, legal and planning aspects.
	3313	Chile, recovery and conservation program for Juan Fernandez endangered plants.
	3315	International, Botanic Gardens Conservation Strategy.
	3320	Sri Lanka, conservation of indigenous medicinal plants.
	3321	Nepal, inventory for *Plant Red Data Book*.
	3325	Southeast Asia, utilization and conservation of palms in India, Malaysia, Indonesia, and Philippines.
	3326	Spain, Isla de la Palma, plant conservation.
	3327	Spain, Canary Islands, plant conservation.
	3328	Mexico, Sierra de Manantlán, wildlife research and management.

TABLE 1. Continued.

Status	Project number[1]	Title
Ongoing	3329	International, preparation of *Plant Conservation—Principles and Practice*.
	3331	International, medicinal plants conservation (with 9201).
	3332	Papua New Guinea, Ethnobotany among the Pinai.
	3333	International, preparation of booklet on in situ conservation of crop relatives, with IBPGR.
	3645	Kenya, floristic survey of the Kaya forest.
	3733	Chile, strategy for conservation of Alerce.
	3781	Algeria, reintroduction and sustainable use of *Cupressus dupreziana*.

[1] This list does not include the majority of projects on tropical forest conservation supported by the Plants Campaign, e.g., in Indonesia, Cameroon, Honduras, Mexico, Peru, and Madagascar.

[2] Projects in 9000-series are financially administered by IUCN, and those in the 3000-series by WWF.

ORGANIZATION OF THE PROGRAMME

The scientific and institutional foundation for the Programme has been established around four main elements, through which the first phase of the Programme has been implemented:

(1) The Joint IUCN–WWF Plant Advisory Group, composed of some 18 eminent botanists from all over the world, who are providing the broad creative thinking and intellectual guidance needed.
(2) The IUCN Plants Office, at the World Conservation Centre in Gland, Switzerland, which coordinates and further develops the Programme's activities.
(3) The Threatened Plants Unit (TPU) of the IUCN Conservation Monitoring Centre at Kew, U.K., which collects, analyzes and provides data on the conservation status of plants and vegetation worldwide.
(4) The Botanic Gardens Conservation Secretariat, at Kew, which works with the botanical gardens of the world to strengthen their roles in conservation.

With these four elements in place, IUCN and WWF have moved from a position of relative weakness in the field of plant conservation to being recognized as its leading proponents worldwide.

OBJECTIVES AND ACTIVITIES OF THE PROGRAMME

The activities of the Plants Conservation Programme were arranged from the very start around six main objectives, designed to address plant conservation from several directions. These objectives are: spreading the message; building the capacity to conserve; conserving plant genetic resources; conserving wild plants of economic value; strengthening the role of botanic gardens in conservation; and promoting plant conservation in selected countries.

The first objective, *spreading the message*, is about awareness and education. The first main element was the 18-month Plant Campaign mounted by WWF in 1984–1985. The participants focused on plants in their publicity and information materials; they produced leaflets, advertisements, an audio-visual, *Saving the Plants that Save Us*, and an excellent popular book by Anthony Huxley on plant conservation, *Green Inheritance*. Many of the 23 WWF national organizations launched their own plants awareness campaigns and programs, developing their own materials or adapting those of the international Plants Campaign to their local needs.

The WWF Plants Campaign was, so to speak, the shop window of WWF for a certain period, thereby also serving to raise the funds to be invested in the Plants Conservation Programme. Since then, the Programme has included a large project in India to alert the people to the importance of

conserving plants; two more, general projects are under way: one, designing a template textbook on biology with emphasis on conservation and development, and the other, initiating a major program on helping botanic gardens become better educators.

There has been a strong effort to reach special audiences, such as the botanic gardens of the world, through conferences or symposia on specific subjects.

The second objective, *building the capacity to conserve*, covers much of the conceptual work needed in plant conservation. Included here is the creation of and the work of the IUCN–WWF Plant Advisory Group and the substantial program of the Threatened Plants Unit (TPU) of the IUCN Conservation Monitoring Centre (see Davis, this volume). A major project of the TPU is preparation of a *Plant Sites Red Data Book*, which will identify the most important sites in the world for conservation of plant diversity, and which will prepare a strategy and rationale for their conservation, thereby providing the most important targets for plant conservation for the next 20 years. Whereas little may be known about individual species, particularly in the tropics, botanists around the world generally have a good idea about which areas matter most for plants. It is far easier, for example, to identify the most important sites in a country than to pinpoint individual threatened plant species. By protecting sites, whole communities can be saved without necessarily requiring all the species to be identified. The *Plant Sites Red Data Book* will be a directory including about 150 botanical sites around the world that IUCN considers to be indicative of those where the most plants can be saved. This directory will serve to bring plant priority areas to the attention of conservation organizations, aid agencies, and governments so that action can be taken to conserve them.

One project is preparation of a book on *Plant Conservation—Principles and Practice*, by Dr. D. Given, being written under the guidance of the Plant Advisory Group. It will be translated and adapted for various cultural and linguistic regions of the world, along the template model.

Conserving plant genetic diversity is the third objective of the Programme. It follows directly from the World Conservation Strategy that IUCN and WWF have a global concern to preserve as much biodiversity as possible. The perspective is much wider than that of most other organizations concerned with genetic resources, such as the Food and Agriculture Organization of the United Nations (FAO) and the International Board for Plant Genetic Resources (IBPGR). The Plants Conservation Programme is concerned with crop plants and their wild relatives and with many thousands of plants with potential value as genetic resources. Emphasis is being placed on in situ conservation, which has been neglected, especially for wild relatives of crops.

The Plants Conservation Programme prepared part of the documentation for the first session of the FAO Commission on Plant Genetic Resources (March 1985) and participants in the Programme attended that session and the second session (1987), giving detailed presentations on IUCN's and WWF's positions on the issues addressed. IUCN's interest also helped create a special working group on in situ conservation of plant genetic resources under the Ecosystems Conservation Group, comprising the United Nations Environment Programme (UNEP), FAO, the United Nations Educational, Scientific and Cultural Organization (Unesco), and IUCN (and in the working group also IBPGR). This provides a way of working toward a common program with the UN bodies concerned. As part of this common work, various information leaflets and booklets are being produced, designed to explain the issue to IUCN members and to the political constituencies of the UN organizations.

Exploring the ideas in the field is the basis for a joint project with IBPGR on mangoes (*Mangifera*) in Borneo and peninsular Malaysia, aiming at investigating the extent to which genetic diversity of *Mangifera* is conserved in protected areas. IUCN and WWF are also supporting projects on wildlife research and management in the proposed biosphere reserve in Sierra de Manantlán, Mexico. The reserve contains a remarkable diverse blend of species of neotropical and nearctic origin, and the occurrence of the perennial diploid maize, *Zea diploperennis*, there makes the reserve a world priority for in situ conservation of a unique genetic resource.

The fourth objective, *conserving wild plants of economic value*, reflects the belief that it is necessary to give proper priority to plants of demonstrated or potential economic value, rather than

giving equal importance to every species. The economic plants conservation effort has two major initiatives: One is development of a "List of Economic Plants for Conservation and Development," which will include species of sufficient importance for human welfare for priority conservation attention. It is believed that such a list may include 5,000–10,000 species, and that the list could become the cornerstone of IUCN's and WWF's program on conservation of economic plants. The second initiative focuses on medicinal plants, a group selected for its tremendous importance in developing countries. Collaboration has been established with the World Health Organization (WHO) to bring together conservationists and health care professionals into a dialogue and to prepare guidance on how each country best can conserve and utilize its medicinal plant resources. Additionally, a field project is under way in Sri Lanka, with the Sri Lankan Ministry of Indigenous Medicine, aiming at in situ conservation and ex situ cultivation of medicinal plants, to secure the long-term supply of the medicinal plants used in the traditional Ayurvedic medicinal system.

Strengthening the roles of botanic gardens in conservation is the fifth objective of the Programme. In recent years botanic gardens have undergone great changes and are keen to change their image. More and more, they see plant conservation as a principal reason for their existence. In developing countries, conserving plant genetic resources and finding ways to make better use of wild plants make the modern botanic garden a vital part of national development.

Working with the botanic gardens of the world has emerged as one of the most successful parts of the Programme, and an area where the Programme has moved far beyond its original scope. As part of the Programme, a conference was organized in the Canary Islands, November 1985, on the theme "Botanic Gardens and the World Conservation Strategy." Botanic gardens around the world were invited to discuss how best to collaborate and to work with IUCN and WWF for plant conservation. As part of the World Conservation Strategy, a draft "Botanic Gardens Conservation Strategy" had been prepared for IUCN and WWF by Professor Vernon H. Heywood and was presented to the conference. The meeting strongly endorsed this draft strategy and asked IUCN to assist gardens in setting up an international mechanism to enable them to work better in a more coordinated way. As a result, and following generous donations from several foundations and corporations, IUCN on 1 January 1987 created the Botanic Gardens Conservation Secretariat, under the leadership of Professor Heywood. This new secretariat brings together a whole new constituency for conservation, covering about 1,400 institutions with at least 100 million visitors annually. A prospectus of the new secretariat has been published (IUCN, 1987) and distributed to the gardens of the world; already during the first half-year of existence, diverse important activities have been initiated and greeted with enthusiasm by the garden community.

The sixth objective is *promoting plant conservation in selected countries*. Aiming at balancing the conceptual and strategic projects, the Plants Conservation Programme includes a growing number of on-the-ground field projects. Since IUCN and WWF cannot realistically develop and implement projects all over the world, 24 countries were selected on criteria of biological importance and of operational, political, and socioeconomic considerations. The countries selected are mostly tropical, reflecting the far greater biological diversity and great threats to the natural vegetation in tropical areas compared with temperate ones.

The field projects tend to fall into two types. The first type involves long-term projects to secure large protected areas for plant-rich sites. These are mainly the continuation of existing IUCN–WWF projects initiated and coordinated by the Tropical Forest Programme. Support comes in many forms, but the emphasis is on developing management plans and infrastructure, rather than providing equipment (such as vehicles), though equipment is often included. WWF is committing about 2.5 million dollars (U.S.) per year to these projects, which include projected area system plans in Cameroon, Borneo, and Irian Jaya and include technical aid projects to consolidate major protected areas, such as Tai (Ivory Coast), Air and Tenere (Niger), Manu (Peru), La Amistad (Costa Rica), Río Platano (Honduras), and certain sites in Madagascar. For example, the Manu National Park in Peru comprises a rainforest bigger than Northern Ireland with more birds and probably more plants than any other park on earth. Another typical example is Sri Lanka, where the IUCN–WWF

involvement through the Plants Conservation Programme has served to bring together the national organizations and agencies responsible for conserving the Sinharaja Forest, which is the last remnant of tropical lowland forest in the country, harboring about 50% of the endemic plants of Sri Lanka, which are of outstanding scientific interest. A new management plan has been worked out and approved by the government, and implementation in the field has started.

The second type comprises plant projects designed to contribute to wider conservation efforts. This includes projects aimed at conserving endemic and threatened floras, for example, production of National Plant Red Data Books for Nepal, Mauritius, and Rodrigues; propagation and reintroduction of endangered species in the Canary Islands; and survey of plant-rich sites in the Ulugurus and Usambaras of East Africa. In some places, in situ and ex situ measures are necessary. In Mauritius, for example, a project is under way in which intensively managed pilot reserves have been established in key areas on the island (Fig. 1) and on its dependency, Rodrigues, and where rare and endangered species have been identified, rescued, and propagated (Fig. 2). The project has generated great interest for conserving the indigenous flora and vegetation, and with active collaboration of the Mauritian Forestry Service, nursery facilities have been established.

A number of projects deal with floristic and botanical surveys. Typically, such projects are intended to provide the basic knowledge on which to formulate more comprehensive conservation plans for certain areas or plants groups. There are, for example, surveys of multipurpose palm species in Latin America and in Southeast Asia, of the plant genetic resources of Socotra Island (Yemen), of medicinal plants of Siberut Island (Indonesia), and inventory and assessment of the unique campo rupestre vegetation in Brazil.

Conclusions

After three years, the first phase of the Plants Conservation Programme is nearing completion. This has been a phase where IUCN and WWF have worked with leaders in the botanical community in developing key concepts for conserving plants, and testing the concepts in the field through model projects. One clear lesson has been that the concepts developed during 20 years or so on animal conservation do not work well for plants. The most successful projects in the Programme have involved going back to the botanical science and thinking out new approaches on that basis. Combining intellectual, scientific work with field projects to look at the practical implications has proved to be effective. The catalytic effect of the Programme—persuading other organizations to work for the same goals and to provide them with the tools to do so—has become evident, e.g., in dealing with plant genetic resources and their in situ conservation, and in collaboration with the botanic gardens of the world.

A second phase of the Programme will involve building on the lessons learned so far, using such tools as the *Plant Sites Red Data Book*, the "List of Economic Plants for Conservation and Development," and the "Botanic Gardens Conservation Strategy," thereby aiming at involving other bodies and organizations on a much larger scale, for example, through cooperation with development aid agencies. The Programme, with its six broad objectives, may also serve as a model for plant conservation on a more local or national scale, such as in the Galápagos. There is a need to raise the awareness about the importance of the Galápagos flora and vegetation, particularly locally in the archipelago. Many of the problems facing the National Park Service and the local farmers in managing the park and the colonized zone have common roots, and have to be dealt with on a common understanding of the issues involved.

As a prerequisite for conserving the flora and vegetation of the Galápagos Islands, it is necessary to build the capacity for plant conservation there. This involves basic and applied botanical research, creation of a database for conservation, preparation of vegetation maps, and other tasks, which together can form the foundation for action.

The endemic Galápagos tomato, *Lycopersicon cheesmanii*, has contributed genes to the culti-

FIGURE 1. Fencing of the newly established Mondrain Nature Reserve, Mauritius, excludes introduced deer and pigs, which are main threats to the indigenous vegetation. (Photo taken in 1986.)

vated tomato, improving the latter for mechanical harvesting (pedicel characters from *L. cheesmanii*) and for transportation (skin characters from *L. cheesmanii*) (Prescott-Allen & Prescott-Allen, 1983). So conservation of plant genetic resources is also an issue of importance in the islands, where other potential genetic resources may be discovered, e.g., among the Leguminosae or the Malvaceae.

An increasingly important question in the Galápagos is the conservation and sustainable utilization of indigenous plants of economic value, particularly trees for construction, firewood, fenceposts, and other purposes. The first experiments for cultivating such useful native species were started a few years ago by the National Park Service and the Charles Darwin Research Station (Fig. 3); it is hoped that eventually a comprehensive plan for in situ conservation of native, economic plant resources will be elaborated and implemented.

FIGURE 2. The Mauritian Forestry Service provides facilities for propagating rare and endangered native species as part of the plant conservation activities in the country. (Photo taken in 1986.)

With more than 90% of the land surface of the archipelago as national park, the concept of ex situ conservation by botanic gardens does not seem to be a priority. However, as Thibodeau pointed out (pers. comm.), there may well be compelling reasons for initiating an ex situ program for some highly threatened species through one or more suitable botanic gardens outside the archipelago. They have the knowledge and the expertise to cultivate, propagate, and eventually reintroduce them to the natural habitats.

Promotion of plant conservation in selected areas is extremely relevant and urgent on the Galápagos Islands scale. As amply documented by several authors in this volume, there is a great need for setting priorities to focus attention and conservation action on particularly threatened areas or vegetation types within the archipelago, such as *Scalesia* forests, *Miconia* scrub, and *Sphagnum* bogs.

FIGURE 3. Experiments are under way in the Galápagos Islands for growing indigenous hardwoods, such as *Piscidia carthagegenensis*, which in places is becoming rare because of over-exploitation. (Photo taken in 1984.)

In order to achieve the long-term conservation of the unique flora and vegetation of the Galápagos Islands, a large-scale and much more concerted effort than before has to be launched. The Workshop on Botanical Research and Management in the Galápagos in April 1987 represents a first, basic step towards this goal.

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COMBINED RECOMMENDATIONS FROM THE WORKSHOP: BOTANICAL RESEARCH AND MANAGEMENT IN GALAPAGOS

Jonas E. Lawesson, Ole Hamann and Juan Black

Based on five White Papers presented to the Workshop and on the SPNG's operational framework for managing the resources of the Galápagos National Park, a set of recommendations was formulated, addressing management of flora and vegetation, research areas to be promoted, and botanical inventories, mapping, and conservation systems.

The list of recommendations presented below, which were edited by the authors, gives a very summarized version of the deliberations approved at the final closing session.

A. *Activities under the National Park's program on eradication of introduced animals.* It is recommended:

—that all efforts should be made to ensure final eradication of feral goats on the island of Pinta. After more than 15 years of dedicated work by the SPNG, over 40,000 goats have been eliminated on this island and only a handful now remain. Complete removal will signify a major success for conservation.

—that feral pigs and goats be controlled and eventually eradicated on the island of Santiago. A great number of rare and endemic plants are being pushed close to extinction, and unique vegetation types are virtually disappearing.

—that constant control and monitoring of feral goats be carried out on Volcán Alcedo, Isabela Island. The presence of goats on Alcedo is a potential threat to the whole uninhabited northern part of Isabela.

—that feral goats be controlled and eventually eradicated in the northern part of San Cristóbal Island. The increasing impact of feral goats threatens numerous rare and endangered plants with extinction.

—that domestic animals be removed from National Park areas on the island of Floreana. Particularly in the highland region, domestic animals aggravate the threat of alien invasive plants to the remaining native plant species and vegetation.

B. *Activities under the National Park's program on eradication of introduced plants.* It is recommended:

—that a department of introduced plants is established at CDRS to coordinate the control of alien species, to undertake such projects as mapping of alien plants on all islands and prevention of further introduction, and to consider the use of biological control in the long term.

—that the control and eradication program on the invasive alien plants *Cinchona succirubra* and *Psidium guajava* in the highlands of Santa Cruz be continued and strengthened.

—that the invasive alien plant *Lantana camara* be controlled and if possible eliminated, particularly on the island of Floreana. *Lantana camara* is rapidly overrunning and replacing the native vegetation types, including species unique to Floreana, and is destroying the largest remaining nesting site of the Galápagos dark-rumped petrel.

—that a program be initiated to control the invasive alien plant *Eugenia jambos* on the island of San Cristóbal, where this species and *Psidium guajava* pose the greatest threat to the last remnants of indigenous vegetation.

—that a program be initiated to control the invasive alien species of Passifloraceae, which are

invading several places in the archipelago, particularly the transition zone vegetation, where alien plants until now have had no serious impact.

C. *Activities under the National Park's program on protection of endangered species.* It is recommended:

—that endangered plant taxa and vegetation types be protected by means of fencing and/or establishment of exclosures to block introduced herbivores and to secure representative samples of indigenous vegetation types, which can serve as living seed banks. Specifically the following areas, taxa, and vegetation types were recommended for priority action:

Santiago Island, James Bay, Cerro Colorado; fencing the hill specifically to protect *Galvezia leucantha* and *Scalesia atractyloides*.

Santa Cruz, Punta Nuñez; fencing to protect *Scalesia retroflexa* and *Froelichia juncea*.

San Cristóbal, Cerro Verde; fencing to protect *Lecocarpus darwinii* and *Calandrinia galapagosa*.

San Cristóbal, Punta Pitt; fencing to protect *Scalesia incisa, Lecocarpus darwinii, Calandrinia galapagosa,* and *Nolana galapaguensis*.

Floreana, Punta Cormorant; fencing to protect *Alternanthera nesiotes, Scalesia villosa,* and *Opuntia megasperma*.

Santiago, San Cristóbal, Floreana, and Santa Cruz highlands; establishment of fenced exclosures to preserve representative samples of vegetation types.

Santa Cruz, South Slope and San Cristóbal, North Slope; investigate long-term possibility for restoration of the complete altitudinal gradient of major vegetation types, e.g., establishing an uninterrupted vegetation corridor from coast to summit. The first initiative in this direction should be restoration in select places of the almost extinct Brown Zone vegetation on Santa Cruz and the highly threatened *Miconia* Zone vegetation on San Cristóbal.

Isabela, Volcán Alcedo; establishment of 3–5 exclosures along the altitudinal gradient to conserve the spectrum of vegetation types.

D. *Documentation System.* Several Galápagos plants are threatened or can soon become so. It is therefore necessary to create a monitoring and documentation system on rare and common species in order to have the background for future conservation and management measures. It is therefore recommended:

—that a complete list of threatened Galápagos plants, preferably as a comparative database, be maintained and continuously updated.

—that a subsidiary but separate list of potential candidate species be compiled in order to recognize plant taxa in need of conservation action before they become threatened.

—that a progressive assessment of status be prepared for all endemic and nonendemic species, based on island distribution, archipelago distribution, and world distribution.

—that a record-keeping system be established to deal with site-specific information of relevance to the above recommendations.

—that a mapping system for individual species is completed for the Galápagos Islands. Such maps should be available as basic reference at the CDRS and SPNG.

—that a monitoring system for threatened plants be developed and implemented to allow the periodic monitoring of taxa at the site and population level.

—that a computer database including all available data from the above recommendations be established at CDRS/SPNG.

—that the community inventories be combined by CDRS/SPNG and visiting scientists and that the existing published and compiled material be treated numerically. And that the system of permanent quadrats be combined and expanded so that more representative plant communities are covered and the information provided for monitoring and conservation efforts.

E. *Mapping program for Galápagos Islands.* A great need for various types of topographical and vegetation maps is recognized, given that such maps form the necessary basis for scientific investigations and conservation and management efforts. It is therefore recommended:

—that all islands receive a complete coverage with high-quality aerial photographs.

—that when the above has been achieved, detailed topographic maps of all islands at a scale of 1:50,000 be completed.

—that based on the two suggestions above, detailed vegetation maps of all islands be prepared in a scale of 1:50,000.

—that the possibilities of establishing a cartographic unit at the CDRS be considered.

—that the various initiatives from cartographic institutions (Germany, Denmark, Japan) to execute mapping in Galápagos be endorsed, provided that CDRS/SPNG are given full authority coordinating and executing the work in general, and especially in the production of vegetation maps, given their long-term research efforts in vegetation studies.

—that fixed photo points be established in key areas of vegetation, and that photographs be taken at regular intervals and deposited at the CDRS.

F. *Ex situ conservation outside Galápagos.* Full recovery plans for a number of endangered plants of the Galápagos should include ex situ conservation, which offers insurance against complete extinction as well as research opportunities and plant material that could be of great value to management of wild populations. A program of ex situ conservation outside Galápagos should therefore be established giving highest priority to taxa at global risk of extinction, not believed to survive in the wild under present conditions. It is therefore recommended:

—that a committee of advisors to guide, program, and design implementation be appointed.

—that collection and management protocols, including documentation, insuring the physical safety of wild populations and the biological quality of the collections be designed.

—that after implementation of the two suggestions above, the ex situ conservation outside Galápagos be initiated in close cooperation with two or three carefully selected botanical gardens, with detailed agreements on mutual responsibilities. The agreements should be long-term to maximize ex situ conservation.

G. *Important research areas to be promoted.* The Workshop considered areas of research thought to be important for scientists (especially nonresidents) who wish to contribute to the high goals of conservation biology and management in the Galápagos Islands. The following list contains some neglected as well as some currently pursued areas of particular relevance:

Plant demography. Demography should be given high priority since almost no investigations have been carried out in Galápagos. A recommended starting point is rare plant species, to find out why they are rare, and species which appear to be key species in ecosystems.

Physiological ecology. Studies on cactus metabolism stand out as a rare contribution to this area. There are almost no investigations on in situ physiological properties of plant species to help us understand their population sizes and distributions.

Phenology. Data on the timing of reproductive and nonreproductive events of plant species are accumulating very slowly. Plant phenology itself has been given very little direct attention, yet it could easily be investigated with minimal cost.

Plant–animal interactions. The influence of animal species on plant species in Galápagos is poorly known. Animals pollinate flowers, disperse seeds, and consume fruits and leaves. Interactions may be very complex, being pronounced and direct or subtle and indirect. By ignoring such interactions it may be very difficult to understand, for example, why some plant populations are declining.

Ecology of plant diseases. Special types of interactions occur among plants and nonanimal enemies, such as fungi. The effects of diseases on plants, the degree to which species are vulnerable to disease organisms, and the frequency of disease attacks on plants are poorly known in plant

ecology in general. Galápagos provides excellent potential for investigations on this important topic.

Plant chemistry. Since plants are eaten by animals, one important aspect of their biology is the type of chemical defense that is used, or not used, to deter consumers. There are no published studies from Galápagos of the chemical defenses of leaves against defoliating insects.

Genecology or ecological genetics. Neglected in Galápagos, this area is important because it helps us to understand the adaptability of plant species, their past adaptations, and their potential for future adaptations through human-induced or natural processes.

Pre-historical ecology. The pioneering studies on the interpretation of past climates and vegetation through palynological research should be extended. They provide a long-term perspective on vegetation change. Many details are still lacking.

Systematics and taxonomy of particular problem groups. Systematics and taxonomy are relatively advanced disciplines for Galápagos plants, but many problems remain to be solved. Several groups of vascular plants, as well as algae, fungi, bryophytes, and lichens need special attention.

Phytogeography. As knowledge of island floras improves, it will become possible to interpret patterns of distribution in the Galápagos, to understand why the archipelago has its particular set of species, and how the patterns of distribution differ from those in other archipelagoes.

Ecology of communities and ecosystems. Of particular relevance in relation to natural macro-events, such as El Niño, volcanism, and droughts.

Ecology of production and nutrient cycling. Another gap in our knowledge of Galápagos plants concerns the large-scale processes that determine the dynamics of ecosystems. A comparative study of different ecosystems along an altitudinal transect on one of the higher islands would be especially valuable. Such studies should complement the various areas of research in community ecology.

H. *Management of sustainable resources*. It is recommended:

—that research in agricultural production and marketing be reoriented, expanded, and intensified.

—that participation of researchers, development planners, execution agencies, and users be sought in developing comprehensive solutions in relation to the management of natural resources.

—that an extensive training program be implemented for SPNG personnel, for the Agricultural Center, Municipalities, Agricultural and Livestock Production Service Agencies, INGALA, and users in general.

—that legal enforcement action be provided to stop expansion of agricultural areas within the National Park, once all farming land has been occupied.

—that production and productivity be increased within the colonized areas.

—that existing organizations be encouraged and strengthened in order to harmonize demands from the public and the private sector.

—that the Galápagos National Park Service pay more attention to problems arising in the agricultural and livestock production zones.

—that chairmanship of the Agriculture and Livestock Production Administration for the Province of Galápagos remain with the SPNG Superintendent.

—that physical delimitation be improved and that permanent control of the National Park and agricultural zone limits be established.

—that the National Park plan and execute educational activities in order to alert the population about the risks of fires.

—that as a medium-term strategy, for a period of 10–15 years, timber and wood exploitation within the National Park limits be eliminated.

—that special use area limits be clearly established and marked.

General Recommendations

Work undertaken by the government agency in charge of the management of natural resources within the Galápagos National Park is noteworthy, since eradication programs, control of introduced plant and animal species, and management of tourism have been so effective that this is considered one of the best national parks in the world.

Basic original research by the Darwin Station and current research aimed at solving management problems within the National Park have been the scientific basis upon which the Galápagos National Park Service has developed and the Marine Resource Reserve has been created.

Many large problems remain due to the presence of introduced species, which have become pests, threatening natural ecosystems and even more particularly, threatening Galápagos agricultural and livestock production.

An ever-increasing number of tourists visiting the islands could in the near future overwhelm the present system of government control, and a potential overflow in the number of visitors could cause serious problems to native vegetation and animal species present on the archipelago and to the National Park visitor sites. Socioeconomic problems to the local population could result.

It is considered:

—that the government of Ecuador has followed a stable policy with respect to management in Galápagos under the principles of conservation.

—that it is a duty of the international scientific community to support such a policy.

—that due to such policy, it has been possible to manage tourism and give special attention to problems affecting the National Park.

—that it is urgent to propose actions that in the near future will strengthen the conservation policy for the archipelago, with increasing attention to problems within the agricultural and livestock production areas.

We acknowledge the Ecuadorian government for managing natural resources within the National Park, keeping those resources for the use of mankind. We support such action through the recommendations and projects discussed during this meeting. Recognizing that it is necessary to increase economic growth in the Galápagos Islands, participants of the Workshop "Botanical Research and Management in Galápagos" recommend to the Ecuadorian government:

—to avoid an increase in the annual number of tourists visiting the islands to a level that exceeds their capacity, causing damage to the unique natural resources in the archipelago. In view of the limited capacity of the islands to receive massive tourism, and due to the scarce amount of fresh water available and the absence of infrastructure for the treatment and purification of water, it would be more convenient to have high-quality, low-quantity tourism as a general strategy for the islands.

—to improve control of the importation of organisms to the islands.

Recognizing the fundamental importance of environmental education in conservation and management, the Workshop strategy endorses the ongoing activities of the environmental education and interpretation group and forwards the recommendations from the meeting for the use of this group in Galápagos.

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